

¹ Increasing prevalence of plant-fungal symbiosis across two
² centuries of environmental change

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Abstract

Species' distributions and abundances are shifting in response to ongoing global climate change. Mutualistic microbial symbionts can provide their hosts with protection from environmental stress. This protection may thus contribute towards resilient responses to environmental change, however these changes may also disrupt species interactions and lead to declines in hosts and/or symbionts. Symbionts preserved within natural history specimens offer a unique opportunity to quantify changes in microbial symbiosis across broad temporal and spatial scales. We asked how the prevalence of seed-transmitted fungal symbionts of grasses (*Epichloë* endophytes), which can protect hosts from abiotic stress, have changed over time in response to climate change, and how these changes vary across host species' ranges. Specifically, we analyzed 2,346 herbarium specimens of three grass host species (*Agrostis hyemalis*, *Agrostis perennans*, *Elymus virginicus*) collected over the past two centuries (1824 – 2019) for the presence or absence of *Epichloë* symbiosis. We found that endophytes increased in prevalence over the last two centuries from ca. 25% prevalence to ca. 75% prevalence, on average, across three host species. Changes in seasonal climate drivers were associated with increasing endophyte prevalence. Notably, increasing precipitation during the peak growing season for *Agrostis* species and decreasing precipitation for *E. virginicus* were associated with increasing endophyte prevalence. We also identified changes in the variability of precipitation and temperature during off-peak seasons as important predictors of increasing endophyte prevalence. Our analysis performed favorably in an out-of-sample predictive test with contemporary survey data, a rare extra step in collections-based research. However, we identified greater local-scale variability in endophyte prevalence in contemporary data compared to what our model could predict based on historic data, suggesting new directions that could improve predictive accuracy. Our results provide novel evidence for a cryptic biological response to climate change that may contribute to the resilience of host-microbe symbiosis through context-dependent benefits that confer a fitness advantage to symbiotic hosts under environmental change.

40

Introduction

41 Understanding how biotic interactions are altered by global change is a major goal of basic and
42 applied ecological research (Blois et al., 2013; Gilman et al., 2010). Documented responses to
43 environmental change, such as shifts in species' distributions (Aitken et al., 2008) and phenology
44 (Piao et al., 2019), are typically blind to concurrent changes in associated biotic interactions.
45 Empirically evaluating these biotic changes – whether interacting species shift in tandem with
46 their partners or not (HilleRisLambers et al., 2013) – is crucial to predicting the reorganization
47 of Earth's biodiversity under global change. Such evaluations have been limited because few
48 datasets on species interactions extend over sufficiently long time scales of contemporary climate
49 change (Poisot et al., 2021).

50 Natural history specimens, which were originally collected to study and preserve taxonomic
51 diversity, present a unique opportunity to explore long-term changes in ecological interactions
52 across broad spatial and temporal scales (Meineke et al., 2018). Natural history collections, built
53 and maintained by the efforts of thousands of scientists, are invaluable time machines, primarily
54 comprised of physical specimens of organisms along with information about the time and place
55 of their collection. These specimens often preserve physical legacies of ecological processes and
56 species' interactions from dynamically changing environments across time and space. For exam-
57 ple, previous researchers have used plant collections (herbaria) to document shifts in phenology
58 (Berg et al., 2019; Park et al., 2019; Willis et al., 2017), pollination (Duan et al., 2019; Pauw and
59 Hawkins, 2011), and herbivory (Meineke et al., 2019) related to anthropogenic climate change.
60 However, few previous studies have leveraged biological collections to examine climate change-
61 related shifts in a particularly common type of interaction: microbial symbiosis.

62 Microbial symbionts are common to all macroscopic organisms and can have important ef-
63 fects on their hosts' survival, growth and reproduction (McFall-Ngai et al., 2013; Rodriguez et al.,
64 2009). Many microbial symbionts act as mutualists, engaging in reciprocally beneficial interac-
65 tions with their hosts that can ameliorate environmental stress. For example, bacterial symbionts

66 of insects, such as *Wolbachia*, can improve their hosts' thermal tolerance (Renoz et al., 2019; Truitt
67 et al., 2019), and arbuscular mycorrhizal fungi, documented in 70-90% of families of land plants
68 (Parniske, 2008), allow their hosts to persist through drought conditions by improving water and
69 nutrient uptake (Cheng et al., 2021). On the other hand, changes in the mean and variance of
70 environmental conditions may disrupt microbial mutualisms by changing the costs and bene-
71 fits of the interaction for each partner, leading the interaction to deteriorate (Aslan et al., 2013;
72 Fowler et al., 2024). Coral bleaching (the loss of symbiotic algae) due to temperature stress (Sully
73 et al., 2019) is perhaps the best known example, but this phenomenon is not unique to corals.
74 Lichens exposed to elevated temperatures experienced loss of photosynthetic function along with
75 changes in the composition of their algal symbiont community (Meyer et al., 2022). How com-
76 monly and under what conditions microbial mutualisms deteriorate or strengthen under climate
77 change remain unanswered questions (Frederickson, 2017). Previous work suggests that these
78 alternative responses may depend on the intimacy and specialization of the interaction as well
79 as the physiological tolerances of the mutualist partners (Rafferty et al., 2015; Toby Kiers et al.,
80 2010; Warren and Bradford, 2014).

81 Understanding of how microbial symbioses are affected by climate change is additionally
82 complicated by spatial heterogeneity in the direction and magnitude of environmental change
83 (IPCC, 2021). Beneficial symbionts are likely able to shield their hosts from environmental stress
84 in locations that experience a small degree of change, but symbionts in locations that experience
85 changes of large magnitude may be pushed beyond their physiological limits (Webster et al.,
86 2008). Additionally, symbionts are often unevenly distributed across their hosts' distribution.
87 Facultative symbionts may be absent from portions of the host range (Afkhami et al., 2014), and
88 hosts may engage with a diversity of partners (different symbiont species or locally-adapted
89 strains) across their environments (Fowler et al., 2023; Fraude et al., 2008; Rolshausen et al., 2018).
90 Identifying broader spatial trends in symbiont prevalence is therefore an important step in de-
91 veloping predictions for where to expect changes in the symbiosis in future climates.

92 *Epichloë* fungal endophytes are specialized symbionts of cool-season grasses, which have been

93 documented in ~ 30% of cool-season grass species (Leuchtmann, 1992). They are transmitted
94 vertically from maternal plants to offspring through seeds. Vertical transmission creates a feed-
95 back between the fitness of host and symbiont (Douglas, 1998; Fine, 1975; Rudgers et al., 2009).
96 Over time, endophytes that act as mutualists should rise in prevalence within a host population
97 (Donald et al., 2021). *Epichloë* are known to improve their hosts' drought tolerance (Decunta
98 et al., 2021) and protect their hosts against herbivores (Crawford et al., 2010) and pathogens (Xia
99 et al., 2018) likely through the production of a diverse suite of alkaloids and other secondary
100 metabolites. The fitness feedback induced by vertical transmission leads to the prediction that
101 endophyte prevalence should be high in populations where these fitness benefits are most impor-
102 tant. Previous survey studies of contemporary populations have documented large-scale spatial
103 patterns in endophyte prevalence structured by environmental gradients (Afkhami, 2012; Bazely
104 et al., 2007; Granath et al., 2007; Sneck et al., 2017). We predicted that prevalence should track
105 temporal changes in environmental drivers that elicit strong fitness benefits.

106 Early research on *Epichloë* used herbarium specimens to describe the broad taxonomic di-
107 versity of host species that harbor these symbionts (White and Cole, 1985), establishing that
108 endophyte symbiosis could be identified in plant tissue from as early as 1851. However, no
109 subsequent studies, to our knowledge, have used the vast resources of biological collections to
110 quantitatively assess spatio-temporal trends in endophyte prevalence and their environmental
111 correlates. Grasses are commonly collected and identified based on the presence of their re-
112 productive structures, meaning that preserved specimens typically contain seeds, conveniently
113 preserving the fungi along with their host plants on herbarium sheets. This creates the oppor-
114 tunity to leverage the unique spatio-temporal sampling of herbarium collections to examine the
115 response of the symbiosis to historical climate change. However, the predictive ability derived
116 from historical analyses is rarely tested against contemporary data (Lee et al., 2024). Critically
117 evaluating whether insights from historical reconstruction are predictive of variation across con-
118 temporary populations is a crucial step for the field to move from reading signatures of the past
119 to forecasting ecological dynamics into the future.

120 In this study, we assessed the long-term responses of endophyte symbiosis to climate change
121 through the use of herbarium specimens of three North American host grass species (*Agrostis*
122 *hyemalis*, *Agrostis perennans*, and *Elymus virginicus*). We first addressed questions describing spa-
123 tial and temporal trends in endophyte prevalence: (i) How has endophyte prevalence changed
124 over the past two centuries? and (ii) How spatially variable are temporal trends in endophyte
125 prevalence across eastern North America? We then addressed how climate change may be driv-
126 ing trends in endophyte prevalence by asking: (iii) What is the relationship between temporal
127 trends in endophyte prevalence and associated changes in climate drivers? We predicted that
128 aggregate endophyte prevalence would increase over time in tandem with climate warming, and
129 that hotspots of endophyte change would correspond spatially to hotspots of climate change.
130 Finally, we evaluated the performance of models built on data from historic specimens with an
131 out-of-sample test, using data on endophyte prevalence from contemporary surveys of host pop-
132 ulations. To answer these questions we examined a total of 2,346 historic specimens collected
133 across eastern North America between 1824 and 2019, and evaluated model performance against
134 contemporary surveys comprising 1,442 individuals from 63 populations collected between 2013
135 and 2020.

136 Methods

137 Focal species

138 Our surveys focused on three native North American grasses: *Agrostis hyemalis*, *Agrostis peren-*
139 *nans*, and *Elymus virginicus*. Both *Agrostis* species host *Epichloë amarillans* (Craven et al., 2001;
140 Leuchtmann et al., 2014), while *Elymus virginicus* typically hosts *Epichloë elymi* (Clay and Schardl,
141 2002). These C₃ grass species are commonly represented in natural history collections with broad
142 distributions covering much the eastern United States (Fig. 1). *A. hyemalis* is a small short-lived
143 perennial species that germinates in spring and typically flowers between March and July (most
144 common collection month: May). *A. perennans* is of similar stature but is longer lived than

¹⁴⁵ *Agrostis hyemalis* and flowers in late summer and early autumn (most common collection month:
¹⁴⁶ September). *A. perennans* is more sparsely distributed, tending to be found in shadier and more
¹⁴⁷ moist habitats, while *A. hyemalis* is commonly found in open and recently disturbed ground.
¹⁴⁸ Both *Agrostis* species are recorded from throughout the Eastern US, but *A. perennans* has a slightly
¹⁴⁹ more northern distribution, whereas *A. hyemalis* is found rarely as far north as Canada and is
¹⁵⁰ listed as a rare plant in Minnesota. *E. virginicus* is a larger and relatively longer-lived species that
¹⁵¹ is more broadly distributed than the *Agrostis* species. It begins flowering as early as March or
¹⁵² April but continues throughout the summer (most common collection month: July).

¹⁵³ *Herbarium surveys*

¹⁵⁴ We visited nine herbaria between 2019 and 2022 (see Table A1 for a summary of specimens in-
¹⁵⁵ cluded from each collection). With permission from herbarium staff, we acquired seed samples
¹⁵⁶ from 1135 *A. hyemalis* specimens collected between 1824 and 2019, 357 *A. perennans* specimens
¹⁵⁷ collected between 1863 and 2017, and 854 *E. virginicus* specimens collected between 1839 and
¹⁵⁸ 2019 (Fig. 1, Fig. 2A, Fig. A1). We chose our focal species in part because they are commonly
¹⁵⁹ represented in herbarium collections, and produce high numbers of seeds, meaning that small
¹⁶⁰ samples would not diminish the value of the specimens for future studies. We collected up
¹⁶¹ to 5-10 seeds per specimen after examining the herbarium sheet under a dissecting microscope
¹⁶² to ensure that we collected mature seeds, not florets or unfilled seeds, fit for our purpose of
¹⁶³ identifying fungal endophytes with microscopy. We excluded specimens for which information
¹⁶⁴ about the collection location and date were unavailable. Each specimen was assigned geographic
¹⁶⁵ coordinates based on collection information recorded on the herbarium sheet using the geocod-
¹⁶⁶ ing functionality of the ggmap R package (Kahle et al., 2019). Many specimens had digitized
¹⁶⁷ collection information readily available, but for those that did not, we transcribed information
¹⁶⁸ printed on the herbarium sheet. Collections were geo-referenced to the nearest county centroid,
¹⁶⁹ or nearest municipality when that information was available. For fifteen of the oldest specimens,
¹⁷⁰ only information at the state level was available, and so we used the state centroid.

171 After collecting seed samples, we quantified the presence or absence of *Epichloë* fungal hyphae
172 in each specimen using microscopy. We first softened seeds with a 10% NaOH solution, then
173 stained the seeds with aniline blue-lactic acid stain and squashed them under a microscope
174 cover slip. We examined the squashed seeds for the presence of fungal hyphae at 200-400X
175 magnification (Bacon and White, 2018). On average we scored 4.7 intact seeds per specimen of
176 *A. hyemalis*, 4.2 seeds per specimen of *A. perennans*, and 3.8 seeds per specimen of *E. virginicus*;
177 we scored 10,342 seeds in total. . Due to imperfect vertical transmission (Afkhami and Rudgers,
178 2008), it is possible that symbiotic host-plants produce a mixture of symbiotic and non-symbiotic
179 seeds. We therefore designated a specimen as endophyte-symbiotic if *Epichloë* hyphae were
180 observed in one or more of its seeds, or non-symbiotic if *Epichloë* hyphae were observed in none
181 of its seeds. To capture uncertainty in the endophyte scoring process, we recorded both a "liberal"
182 and a "conservative" endophyte status for each plant specimen. When we identified potential
183 endophytes with unusual morphology, low uptake of stain, or a small amount of fungal hyphae
184 across the scored seeds, we recorded a positive liberal status (more likely to be endophyte-
185 positive) and a negative conservative status (less likely to be endophyte-positive). 89% of scored
186 plants had matching liberal and conservative scores, reflecting high confidence in endophyte
187 status. The following analyses used the liberal status, but we repeated all analyses with the
188 conservative status which yielded qualitatively similar results (Fig. A8).

189 *Modeling spatial and temporal changes in endophyte prevalence*

190 We assessed spatial and temporal changes in endophyte prevalence across each host distribution,
191 quantifying the "global" temporal trends aggregated across space, and then examining spatial
192 heterogeneity in the direction and magnitude of endophyte change (hotspots and coldspots)
193 across the spatial extent of each host's distribution. To account for the spatial non-independence
194 of geo-referenced occurrences, we used an approximate Bayesian method, Integrated Nested
195 Laplace Approximation (INLA), to construct spatio-temporal models of endophyte prevalence.
196 INLA provides a computationally efficient method of ascertaining parameter posterior distribu-

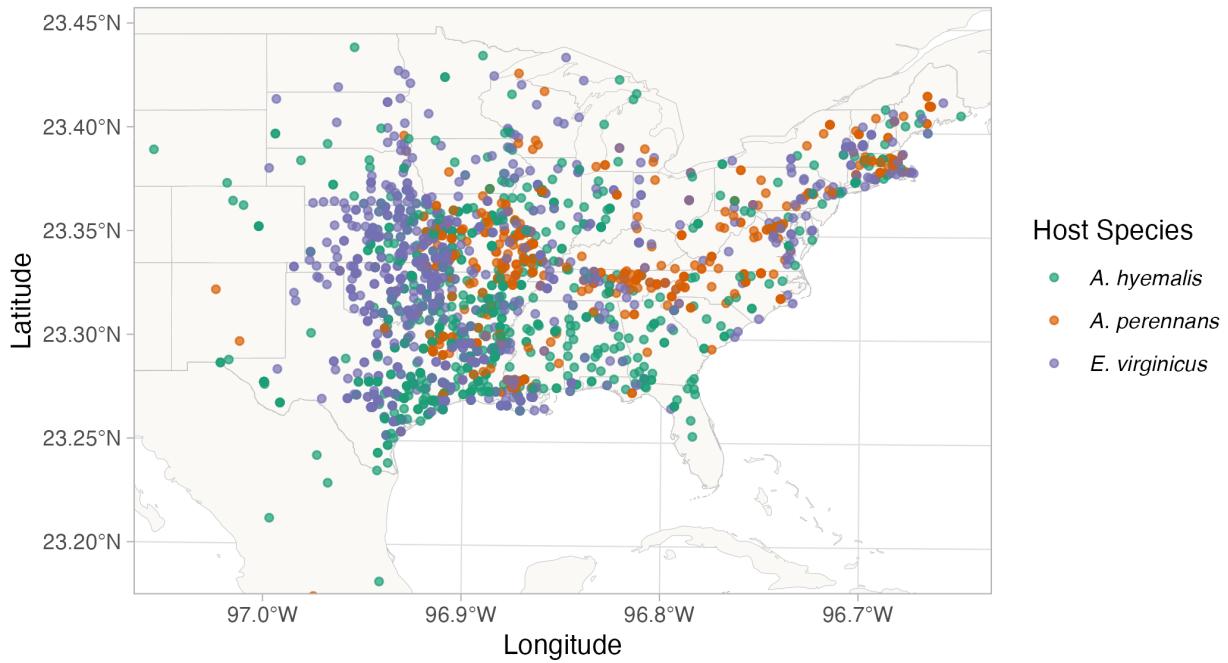


Figure 1: Collection locations of herbarium specimens sampled for *Epichloë* endophytes. Specimens span eastern North America from nine herbaria, and are colored by host species.

197 tions for certain models that can be formulated as latent Gaussian Models (Rue et al., 2009).
 198 Many common statistical models, including structured and unstructured mixed-effects models,
 199 can be represented as latent Gaussian Models. We incorporated spatial heterogeneity into this
 200 analysis using spatially-structured intercept and slope parameters implemented as stochastic
 201 partial differential equations (SPDE) to approximate a continuous spatial Gaussian process. This
 202 SPDE approach is a flexible method of smoothing across space while explicitly accounting for
 203 spatial dependence between data-points (Bakka et al., 2018; Lindgren et al., 2011). Fitting models
 204 with structured spatial effects is possible with MCMC sampling but can require long computa-
 205 tion times, making INLA an effective alternative. This approach has been used to model spatial
 206 patterns in flowering phenology (Willems et al., 2022), the abundance of birds (Meehan et al.,
 207 2019) and butterflies (Crossley et al., 2022), the distribution of temperate trees (Engel et al., 2022)
 208 as well as the population dynamics of endangered amphibians (Knapp et al., 2016) and other

209 ecological processes (Beguin et al., 2012).

210 We estimated global and spatially-varying trends in endophyte prevalence using a joint-
211 likelihood model. For each host species h , endophyte presence/absence of the i^{th} specimen ($P_{h,i}$)
212 was modeled as a Bernoulli response variable with expected probability of endophyte occurrence
213 $\hat{P}_{h,i}$. We modeled $\hat{P}_{h,i}$ as a linear function of intercept A_h and slope T_h defining the global trend
214 in endophyte prevalence specific to each host species as well as with spatially-varying intercepts
215 α_{h,l_i} and slopes τ_{h,l_i} associated with location (l_i , the unique latitude-longitude combination of the
216 i^{th} observation). The joint-model structure allowed us to “borrow strength” across species in
217 the estimation of shared variance terms for the spatially-dependent random effect δ_{l_i} , intended
218 to account for residual spatial variation, and χ_{c_i} and ω_{s_i} i.i.d.-random effects indexed for each
219 collector identity (c_i), and scorer identity (s_i) of the i^{th} specimen.

$$\text{logit}(\hat{P}_{h,i}) = A_h + T_h * \text{year}_i + \alpha_{h,l_i} + \tau_{h,l_i} * \text{year}_i + \delta_{l_i} + \chi_{c_i} + \omega_{s_i} \quad (1)$$

220 By including random effects for collectors and scorers, we accounted for “nuisance” variance
221 that may bias predictions for changes in endophyte prevalence. Previous work suggests that
222 behavior of historical botanists may introduce biases into ecological inferences made from historic
223 collections (Kozlov et al., 2020). Prolific collectors who contribute thousands of specimens may
224 be more or less likely to collect certain species, or specimens with certain traits (Daru et al., 2018).
225 Similarly, the process of scoring seeds for hyphae involved several student researchers who, even
226 with standardized training, may vary in their likelihood of positively identifying *Epichloë*.

227 We performed model fitting using the *inlabru* R package (Bachl et al., 2019). Global intercept
228 and slope parameters A , and T , were given vague priors. Scorer and collector random effects,
229 χ and ω , were given penalized complexity priors, with distributions approximating a Normal
230 distribution with standard deviation of 5. Each spatially-structured parameter depended on a
231 covariance matrix according to the proximity of each pair of collection locations (Bakka et al.,
232 2018; Lindgren et al., 2011). The covariance matrix was approximated using a Matérn covariance
233 function, with each data point assigned a location according to the nodes of a mesh of non-

²³⁴ overlapping triangles encompassing the study area (Fig. A2). We assessed model fit with visual
²³⁵ posterior predictive checks (A3) and measurements of AUC (Figs. A4-A5). Priors for the Matérn
²³⁶ covariance function, termed "range" and "variance", define how proximity effects decay with
²³⁷ distance. Results presented in the main text reflect a prior range of 342 kilometers (i.e. a 50%
²³⁸ probability of estimating a range less than 342 kilometers). We tested a range of values (from 68
²³⁹ kilometers to 1714 kilometers) and meshes (presented in the Supporting Methods), finding that
²⁴⁰ while the magnitude and uncertainty of effects varied, model results were qualitatively similar,
²⁴¹ i.e. the same direction of effects across space.

²⁴² *Modeling distributions of host species*

²⁴³ Because the herbarium records did not encompass the entirety of these host species' ranges,
²⁴⁴ we additionally modeled the geographic distribution of each host species to generate realistic
²⁴⁵ maps on which we could project the predictions of the INLA model. We followed the ODMAP
²⁴⁶ (overview, data, model, assessment, prediction) protocol (Crossley et al., 2022) (see Supporting
²⁴⁷ Methods). In short, we used presence-only observations of each host species from Global Bio-
²⁴⁸ diversity Information Facility (GBIF) between 1990 to 2020. We fit maximum entropy (MaxEnt)
²⁴⁹ models using the maxent function in the R package dismo (Hijmans et al., 2017) using the same
²⁵⁰ set of seasonal climate predictors considered above calculated for the 1990-2020 climate normals:
²⁵¹ mean and standard deviation of spring, summer, and autumn temperature, and mean and stan-
²⁵² dard deviation of spring, summer, and autumn cumulative precipitation. We generated 10,000
²⁵³ pseudo-absences as background points, and split the occurrence data into 75% for model train-
²⁵⁴ ing and 25% for model testing. The performance of models was evaluated with AUC (Jiménez-
²⁵⁵ Valverde, 2012). We found AUC values of 0.862, 0.838, 0.821 respectively for *Agrostis hyemalis*,
²⁵⁶ *Agrostis perennans*, and *Elymus virginicus* indicating good model fit to data. To convert the contin-
²⁵⁷ uous predicted probabilities into binary presence - absence maps on which we projected INLA
²⁵⁸ predictions, we used the training sensitivity (true positive rate) and specificity threshold (true
²⁵⁹ negative rate) (Liu et al., 2005).

260

Assessing the role of climate drivers

261 We assessed how the magnitude of climate change may have driven changes in endophyte preva-
262 lence by assessing correlations between changes in climate and changes in endophyte prevalence
263 predicted from our spatial model at evenly spaced pixels across the study area. We first down-
264 loaded monthly temperature and precipitation rasters from the PRISM climate group (Daly and
265 Bryant, 2013) covering the time period between 1895 and 2020 using the 'prism' R package (Hart
266 and Bell, 2015). Prism provides reconstructions of historic climate variables across the United
267 States by spatially-interpolating weather station data (Di Luzio et al., 2008). We calculated 30-year
268 climate normals for seasonal mean temperature and cumulative precipitation for the recent (1990
269 to 2020) and historic (1895 to 1925) periods. We used three four-month seasons within the year
270 (Spring: January, February, March, April; Summer: May, June, July, August; Autumn: September,
271 October, November, December). This division of seasons allowed us to quantify differences in
272 climate associated with the two "cool" seasons, when we expected our focal species to be most
273 biologically active (*A. hyemalis* flowering phenology: spring; *E. virginicus*: spring and summer; *A.*
274 *perennans*: autumn). In addition to mean climate conditions, environmental variability itself can
275 influence population dynamics (Tuljapurkar, 1982) and changes in variability are a key prediction
276 of climate change models (IPCC, 2021; Stocker et al., 2013). Therefore, we calculated the standard
277 deviation for each annual and seasonal climate driver across each 30-year period. We then took
278 the difference between recent and historic periods for the mean and standard deviation for each
279 climate driver (Figs. A12-A14). All together, we assessed twelve potential climate drivers: the
280 mean and standard deviation of spring, summer, and autumn temperature, as well as the mean
281 and standard deviation of spring, summer, and autumn cumulative precipitation.

282 To evaluate whether areas that have experienced the greatest changes in endophyte preva-
283 lence (hotspots of endophyte change) are associated with high degrees of change in climate
284 (hotspots of climate change), we modeled the fitted, spatially-varying slopes of endophyte change
285 through time ($\tau_{[h]l}$ as a linear function of environmental covariates, with a Gaussian error distri-

bution. Data from each host species was analyzed separately. Fitting regressions to many pixels across the study region risks artificially inflating confidence in our results due to large sample sizes, and so we performed this analysis using only a random subsample of 250 pixels across the study region; other sizes of subsample yielded similar results.

290 *Validating model performance with in-sample and out-of-sample tests*

291 We evaluated the predictive ability of the model using both in-sample training data from the
292 herbarium surveys, and with out-of-sample test data, an important but rarely used strategy in
293 ecological studies (Lee et al., 2024; Tredennick et al., 2021). We generated out-of-sample test
294 data from contemporary surveys of endophyte prevalence in natural populations of *A. hyemalis*
295 and *E. virginicus* in Texas and the southern US. Surveys of *E. virginicus* were conducted in 2013
296 as described in Sneck et al. (2017), and surveys of *A. hyemalis* took place between 2015 and
297 2020. Population surveys of *A. hyemalis* were initially designed to cover longitudinal variation
298 in endophyte prevalence towards its range edge, while surveys of *E. virginicus* were designed to
299 cover latitudinal variation. In total, we visited 43 populations of *A. hyemalis* and 20 populations
300 of *E. virginicus* across the south-central US, with emphasis on Texas and neighboring states (Fig
301 A11). During surveys, we collected seeds from up to 30 individuals per population (average
302 number of plants sampled per population: 22.9); note that this sampling design provided greater
303 local depth of information than the herbarium records, where only one plant was sampled at
304 each locality. We quantified the endophyte status of each individual with staining microscopy
305 as described for the herbarium surveys (with 5-10 seeds scored per individual), and calculated
306 the prevalence of endophytes within the population (proportion of plants that were endophyte-
307 symbiotic). For each population, we compared the observed fraction of endophyte-symbiotic
308 hosts to the predicted probability of endophyte occurrence \hat{P} derived from the model for that
309 location and year. The contemporary survey period (2013-2020) is at the most recent edge of the
310 time period encompassed by the historical observations used for model fitting.

311

Results

312 *How has endophyte prevalence changed over time?*

313 Across >2300 herbarium specimens dating back to 1824, we found that prevalence of *Epichloë*
314 endophytes increased over the last two centuries for all three grass host species (Fig. 2). On
315 average, endophytes of *A. perennans* and *E. virginicus* increased from ~ 40 % to 70% prevalence
316 across the study region, and *A. hyemalis* increased from ~ 25% to over 50% prevalence. Our
317 model indicates a high certainty that overall temporal trends are positive across species (99%
318 probability of a positive overall year slope in *A. hyemalis*, 92% probability of a positive overall
319 year slope in *A. perennans*, and 91% probability of a positive overall year slope in *E. virginicus*)
320 (Fig. A6).

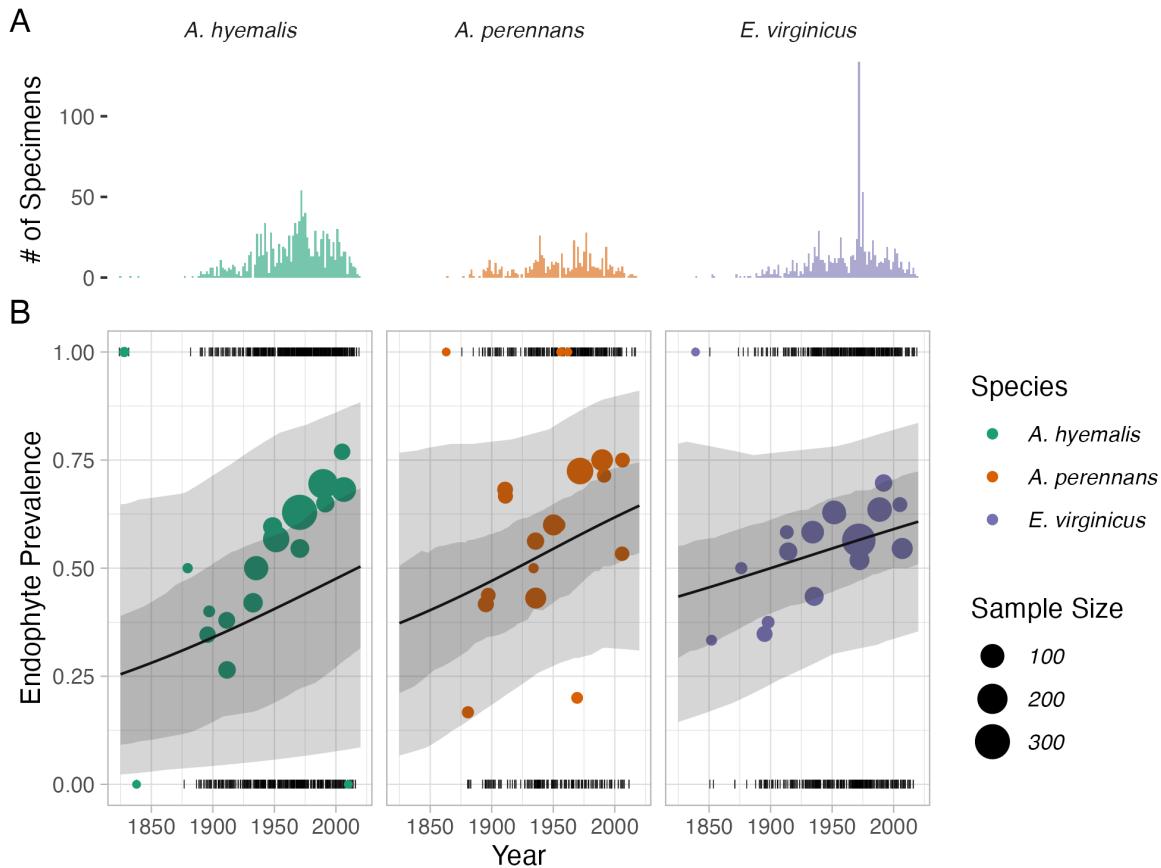


Figure 2: **Temporal trends in endophyte prevalence.** (A) Histograms show the frequency of scored specimens through time for each host species. (B) Lines show predicted mean endophyte prevalence over the study period along with the 50% and 95% CI bands incorporating uncertainty associated with collector and scorer random effects. Colored points are binned means of the observed endophyte presence/absence data (black dashes). Colors represent each host species and point size represents the number of specimens.

321 The model appears to under-predict the observed increase in endophyte prevalence relative
 322 to the data, particularly for *A. hyemalis* (Fig. 2B), but the model is accounting for random effects
 323 and spatial non-independence that are not readily seen in the figure. We found no evidence that
 324 collector biases influenced our results. Collector random effects were consistently small (Fig.
 325 A9), and models fit with and without this random effect provide qualitatively similar results.

326 The identity of individual scorers did contribute to observed patterns in endophyte prevalence.
327 For example, 3 of the 25 scorers were more consistently likely than average to assign positive
328 endophyte status, as indicated by 95% credible intervals greater than zero (Fig. A10). It is
329 difficult to distinguish whether this was driven by true differences in scorers biases during the
330 seed scoring process or by unintended spatial or temporal clustering of the specimens scored by
331 each scorer (Clayton et al., 1993; Urdangarin et al., 2023). By under-weighting endophyte-positive
332 samples that are clustered spatially or by collector or observer, the INLA model is appropriately
333 accounting for nuisance variables and providing a conservative inference of endophyte change
334 relative to the raw data.

335 *How spatially variable are temporal trends in endophyte prevalence?*

336 While there was an overall increase in endophyte prevalence, our model revealed hotspots and
337 coldspots of change across the host species' ranges, which are mapped in Fig. 3 across geo-
338 graphic ranges predicted by MaxEnt species distribution models. In some regions, posterior
339 mean estimates of spatially varying temporal trends indicate that *A. hyemalis* and *A. perennans*
340 experienced increases in prevalence by as much as 2% per year over the study period, while
341 *E. virginicus* experienced increases up to around 1% per year. Both *Agrostis* species show areas
342 of strong increase and areas of declining prevalence, while *E. virginicus* had an overall weaker
343 and geographically more homogeneous increase in endophyte prevalence. Notably, endophytes
344 increased most strongly towards the western range edge of *A. hyemalis* (Fig. 3A) and across the
345 northeastern US for *A. perennans* (Fig. 3B). Posterior estimates of uncertainty in spatially varying
346 slopes indicate that these hotspots of change may have experienced increases of up to 5% per
347 year while declines in prevalence may be as great as 4% per year for *A. hyemalis* and *A. perennans*.
348 For *E. virginicus*, uncertainty ranges between 3.5% increases and 2.5% decreases (Fig. A7).

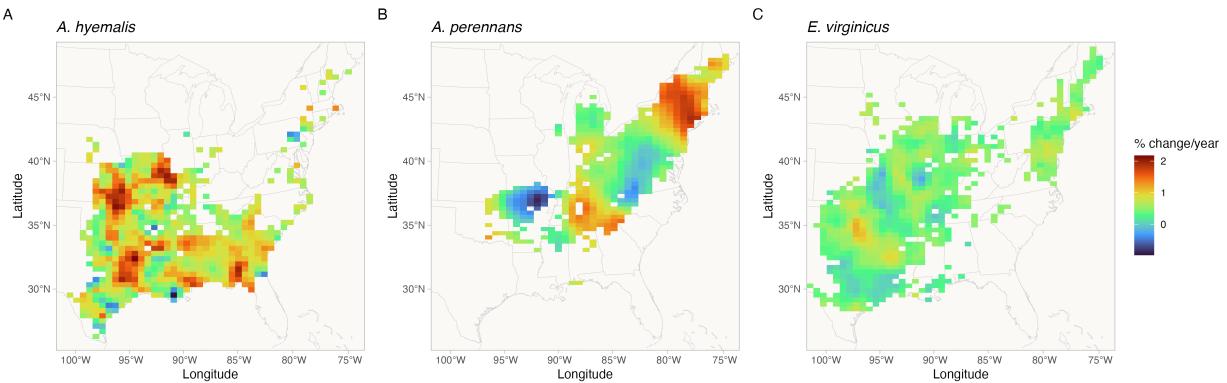


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

What is the relationship between variation in temporal trends in endophyte prevalence and changes in climate drivers?

We found that trends in endophyte prevalence were strongly associated with seasonal climate change drivers (Fig. 4). For the majority of the study region, the climate has become wetter (an average increase in annual precipitation of 60 mm.) with relatively little temperature warming (an average increase in annual temperature of 0.02 °C) over the last century (Fig. A12-A14), a consequence of regional variation in global climate change (IPCC, 2021). Within the region, climate changes were spatially variable; certain locations experienced increases in annual precipitation as large as 375 mm. or decreases up to 54 mm. across the last century, while annual temperature changes ranged from warming as great as 1.4 °C to cooling by 0.46 °C. Spatially variable climate trends were predictive of trends in endophyte prevalence. For example, strong increases in endophyte prevalence for *A. perennans* were most strongly associated with increasing autumn precipitation and with increasing mean and variability in autumn temperature (greater than 97% posterior probabilities of positive slopes). For this species, a 1 °C increase in autumn temper-

ature was associated with a 1.07 % increase per year in endophyte prevalence (Fig. 4A) and a 100 mm. increase in precipitation was associated with a 0.8% increase per year in endophyte prevalence (Fig. 4B). This result aligns with the species' autumn active growing season, however other seasonal climate drivers were also associated with increasing endophyte prevalence. In particular, we found cooler and drier springs and cooler summers to be associated with increasing endophyte prevalence (greater than 99% posterior probabilities of negative slopes) however these slopes were generally of smaller magnitude than those for autumn climate drivers.

Changes in endophyte prevalence across the ranges of *A. hyemalis* and *E. virginicus* were less strongly driven by changes in climate. Like *A. perennans*, climate during peak growing season (spring for *A. perennans* and summer for *E. virginicus*) emerged most commonly as drivers of changes in endophyte prevalence. Increases in mean spring precipitation were the strongest predictor of increasing trends in endophyte prevalence for *A. hyemalis* (Fig. 4B) (greater than 99% posterior probability of a positive slope). For this species, an increase of 100 mm. in spring precipitation led to an increase of 0.6% per year in endophyte prevalence. The next greatest slopes were those associated with variability in spring precipitation (greater than 96% posterior probability of a negative slope), as well as in the mean and variability of autumn climate (greater than 98% probability of negative and positive slopes, respectively). Changes in endophyte prevalence in *E. virginicus* were not strongly associated with changes in most climate drivers, but regions with reduced variability in autumn precipitation (Fig. 4B) and with cooler and more variable summer temperatures (Fig. 4A,C) experienced the largest increases in endophyte prevalence. While our analysis identified the importance of these drivers with relatively high certainty (greater than 99% posterior probability of either negative or positive slopes respectively), they translate to less than 0.2% change in endophyte prevalence per year for a change of 100 mm. change in precipitation over the century. Repeating this analysis using all pixels across each species' distribution were qualitatively similar to these results.

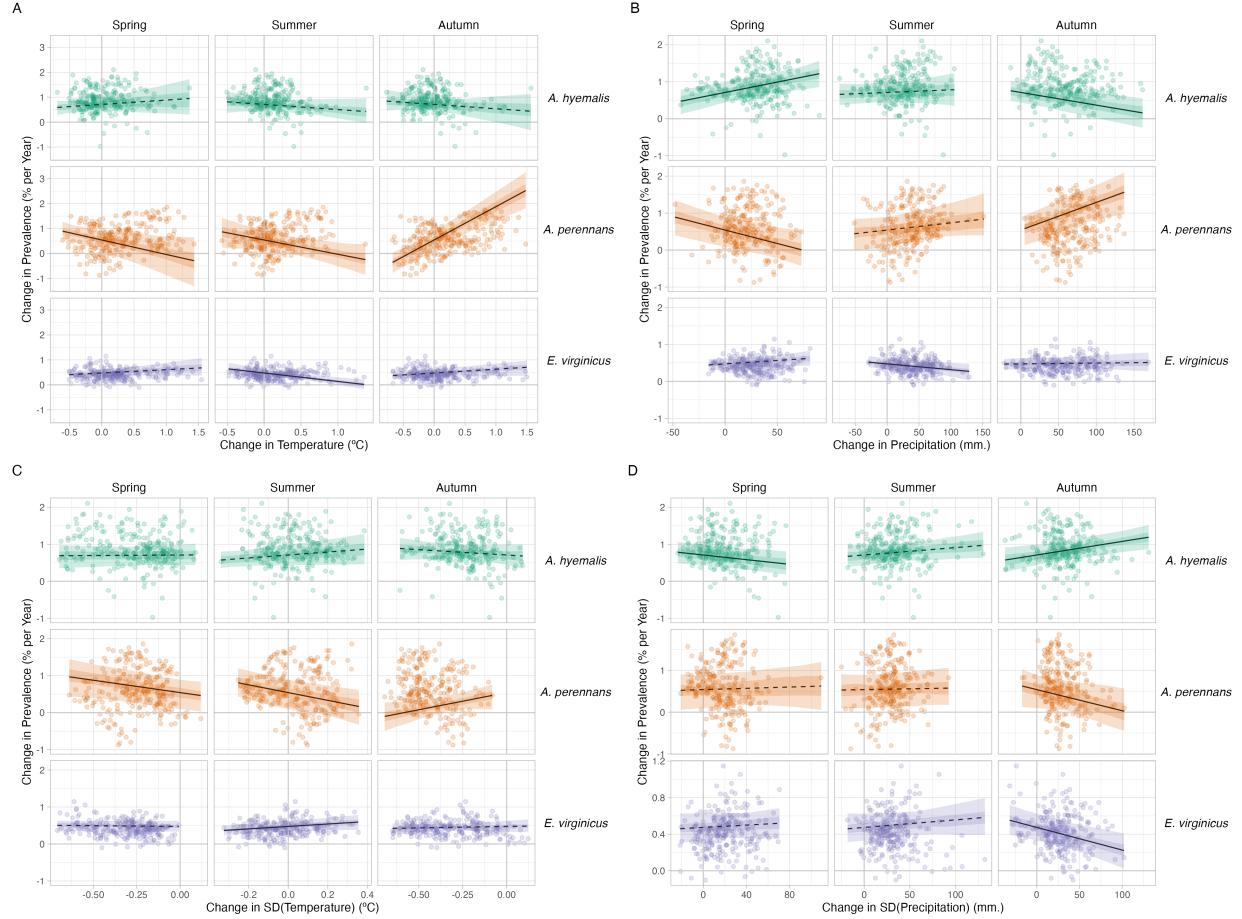


Figure 4: Relationships between predicted trends in endophyte prevalence and changes in seasonal climate drivers. Lines show marginal predicted relationship between spatially-varying trends in endophyte prevalence and changes in mean and variability of climate ((A): mean temperature, (B): cumulative precipitation, (C): standard deviation in temperature, (D): standard deviation in precipitation). Confidence bands represent the 50 and 95% CI, colored by host species. Slopes with greater than 95% probability of being either positive or negative are represented as solid lines while those that have less than 95% probability are dashed. Points show 250 randomly sampled pixels across each host's distribution used in model fitting.

388 *Performance on test data*

389 Tests of model's predictive performance as quantified by AUC and by visual posterior predic-
390 tive checks, indicated good predictive ability. Model performance was similar between historic
391 herbarium specimens used as training data and the out-of-sample test data from contemporary
392 surveys (AUC = 0.79 and 0.77 respectively; Fig. A5-A4). The model successfully captured broad
393 regional trends in endophyte prevalence seen in the contemporary survey data, such as decline
394 endophyte prevalence in *A. hyemalis* towards western longitudes (Fig. 5A) and northern lati-
395 tudes (Fig. 5B). However, model predictions for endophyte prevalence exhibited relatively little
396 local geographic variation, whereas the out-of-sample survey data were maximally variable with
397 populations spanning 0% to 100% endophyte-symbiotic plants (Fig. 5C). We interpret this to
398 mean that the model captures coarse-scale spatial and temporal trends reasonably well, but is
399 not equipped to capture local-scale nuances that generate population-to-population differences.

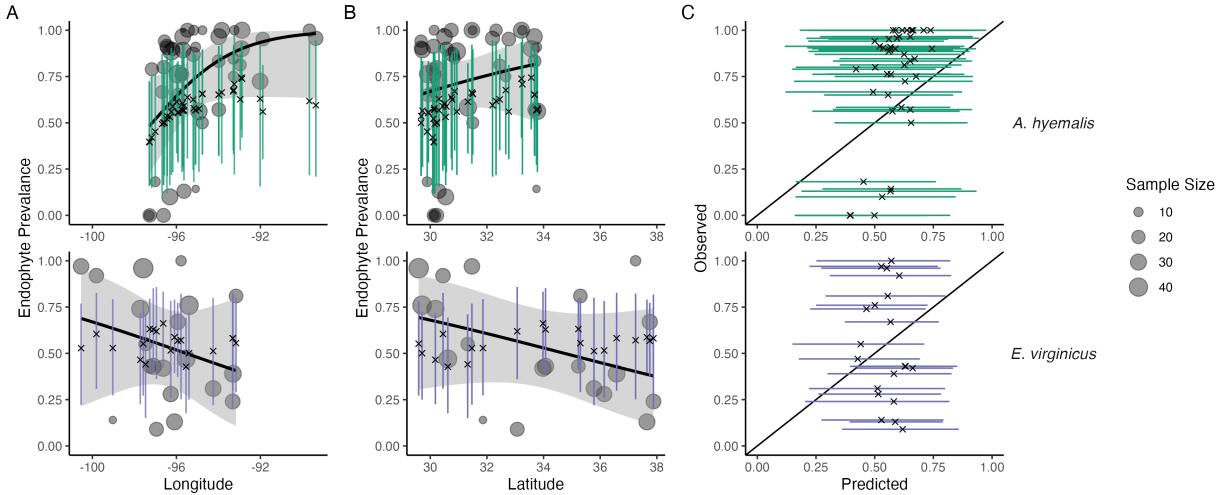


Figure 5: Predictive performance for contemporary test data. (A) The model, trained on historic herbarium collection data, performed modestly at predicting prevalence in contemporary population surveys. The model captured regional trends across (A) longitude and (B) latitude. Crosses indicate predicted mean prevalence along with the 95% CI (colored lines) from the herbarium model. Contemporary prevalence is represented by grey points (point size reflects sample size) along with trend lines from generalized linear models (black line and shaded 95% confidence interval). (C) Comparison of observed vs. predicted endophyte prevalence shows that contemporary test data had more variance between populations than contemporary predictions.

Discussion

Our examination of historic plant specimens revealed cryptic shifts in microbial symbiosis over the last two centuries. For the three host species we examined, there have been strong increases in prevalence of fungal endophytes. We interpret increases in prevalence of *Epichloë*, which are vertically transmitted, as adaptive changes that improve the fitness of their hosts under increasing environmental stress. This interpretation is in line with theory predicting that the positive fitness feedback caused by vertical transmission leads beneficial symbionts to rise in prevalence within a population (Donald et al., 2021; Fine, 1975). We further found that trends in endophyte

408 prevalence varied across the distribution of each species in association with changes in climate
409 drivers, suggesting that the increases in endophyte prevalence are driven by context-dependent
410 benefits to hosts that confer resilience under environmental change. Taken together, this suggests
411 an overall strengthening of host-symbiont mutualism over the last two centuries.

412 Differences across host species underscore that while all of these C_3 grasses share similar
413 broad-scale distributions, each engages in unique biotic interactions and has unique responses to
414 environmental drivers. We identified hotspots of change for *A. perennans*, which was the species
415 that experienced the strongest absolute changes in endophyte prevalence (Fig. 3). Declines of
416 0.9% per year in the southern portion of its range and increases of up to 2% per year in the
417 north suggest a potential poleward range shift of endophyte-symbiotic plants (whether the over-
418 all host distribution is shifting in parallel is an exciting next question). Based on previous work
419 demonstrating that endophytes can shield their hosts from drought stress (reviewed in Decunta
420 et al. (2021)), we generally predicted that drought conditions would be a driver of increasing en-
421 dophyte prevalence. In contrast to this expectation, increasing prevalence for *A. perennans* were
422 associated with increasing autumn temperature and precipitation (Fig. 4). To our knowledge,
423 the response of the symbiosis in *A. perennans* to drought has not been examined experimentally,
424 but in a greenhouse experiment, endophytes had a positive effect on host reproduction under
425 shaded, low-light conditions (Davitt et al., 2010). Our results also hint that it may be useful to
426 investigate whether lagged climate effects are important predictors of host fitness in this system
427 (Evers et al., 2021). Endophyte prevalence of the autumn-flowering *A. perennans* was strongly
428 linked with decreasing spring precipitation, and that of the spring-flowering *A. hyemalis* was as-
429 sociated with decreasing autumn precipitation (Fig. 4B). For *A. hyemalis*, endophytes could be
430 playing a role helping hosts weather autumn-season droughts, which may be an important time
431 for the species' germination. Previous work has demonstrated drought benefits in a greenhouse
432 manipulation with this species (Davitt et al., 2011), and early life stages may be particularly vul-
433 nerable to prolonged droughts. For *E. virginicus*, which experienced the most modest changes
434 in endophte prevalence overall (ranging between 1.1% increases and 0.2% decreases), we only

435 found modest associations with changes in climate drivers. Surveys by Sneck et al. (2017), used
436 as part of the test data in this study, identified a drought index (SPEI) that integrates precipitation
437 with estimated evapotranspiration as an important predictor of endophyte prevalence. *Epichloë*
438 endophytes have also been connected to a suite of non-drought related fitness benefits including
439 herbivore protection (Brem and Leuchtmann, 2001), salinity resistance (Wang et al., 2020), and
440 mediation of the soil microbiome (Roberts and Ferraro, 2015). These effects are potentially medi-
441 ated by the diverse bioactive alkaloids and other signaling compounds they produce (Saikkonen
442 et al., 2013). Increases in symbionts could be explained, at least in part, by these diverse benefits
443 that may help hosts weather a world made increasingly stressful by changes in climate and other
444 anthropogenically introduced stressors. While we show consistent increasing trends in preva-
445 lence between the three species, the mechanisms that explain these changes may be diverse and
446 idiosyncratic.

447 The combination of a spatially-explicit model and historic herbarium specimens allowed us
448 to identify regions of both increasing and decreasing endophyte prevalence, however we see
449 several next steps towards the goal of predicting host and symbiont niche-shifts in response to
450 future climate change. While the model recreated the large-scale spatial trends observed in con-
451 temporary population surveys, test data contained more population-to-population variability in
452 prevalence. Validating our model predictions in this way, a rare extra step in collections-based
453 studies, allows us to evaluate places to improve the model's out-of-sample predictive ability.
454 Lack of information on local variability may simply be a feature of data derived from herbarium
455 specimens. They are samples from local populations, but they are single specimens that are ag-
456 gregated to derive broad-scale model estimates. This suggests that increasing local replication
457 should be a factor considered in future collection efforts of natural history specimens, balanced
458 with the required time and effort. Poor predictive ability at local scales in this grass-endophyte
459 system is not surprising, as previous studies have found that local variation, even to the scale
460 of hundreds of meters can structure endophyte-host niches (Kazenel et al., 2015). Other studies
461 have found factors including land-use history (Vikuk et al., 2019) and the biotic environment,

462 including herbivory (Rudgers et al., 2016), and host genotype Sneck et al. (2017), to be important
463 predictors of endophyte ecology. An important step would be integrating data from local and
464 regional scales through modeling to constrain estimates of local and regional variation. Previ-
465 ous population surveys have found environment-dependent gradients in endophyte prevalence
466 (Rudgers and Swafford, 2009; Semmarin et al., 2015; Sneck et al., 2017), that may be caused
467 by symbiont-derived fitness benefits allowing their hosts to persist in environments where they
468 otherwise could not (Afkhami et al., 2014; Fowler et al., 2023; Kazenel et al., 2015). Predict-
469 ing future niche-shifts of hosts and symbionts will require considering the coupled dynamics of
470 host-symbiont dispersal in addition to fitness benefits. For example, transplanting symbiotic and
471 non-symbiotic plants beyond the range edge of *A. hyemalis* could tell us whether low endophyte
472 prevalence in that area is a result of environmental conditions that lead the symbiosis to negative
473 fitness consequences, or is a result of some historical contingency or dispersal limitation that
474 has thus far limited the presence of symbiotic hosts from a region where they would otherwise
475 flourish and provide resilience. Incorporating available climatic and soil layers as covariates is
476 another obvious step that could improve predictions. These steps will bridge gaps that often
477 exist between large but broad bioclimatic and biodiversity data and small but local data on bi-
478 otic interactions, and move towards the goal of predicting the dynamics of microbial symbioses
479 under climate change (Isaac et al., 2020; Miller et al., 2019).

480 Our analysis advances the use of herbarium specimens in global change biology in two ways.
481 First and foremost, this is the first study to link long-term changes in microbial symbioses to
482 changes in climate using specimens from natural history collections. The responses of micro-
483 bial symbioses are a rich target for future studies within museum specimens, particularly those
484 that take advantage of advances in sequencing technology. While we used relatively coarse
485 presence/absence data based on fungal morphology, other studies have examined historic plant
486 microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these
487 studies have so far been limited to relatively few specimens at limited spatial extents (Bieker
488 et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al.,

489 2015). Continued advances in capturing historic DNA and in filtering out potential contamination
490 during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith, 2021)
491 will be imperative in the effort to scale up these efforts. This scaling up will be essential to be
492 able to quantify changes not just in the prevalence of symbionts, but also in symbionts' intraspecific
493 variation and evolutionary responses to climate change, as well as in changes in the wider
494 microbial community. Genetic variation in *Epichloë* endophytes, particularly in genes responsible
495 for alkaloid production, produces "chemotypes" with differing benefits for hosts against
496 insect or mammalian herbivores mediated by environmental conditions (Saikkonen et al., 2013;
497 Schardl et al., 2012). With improved molecular insights from historic specimens, we could ask
498 whether the broad increases in endophytes that we have identified reflect selection for particular
499 chemotypes and how this selection varies across space. Answering these questions as well as
500 the unknown questions that future researchers may ask also reiterates the value in capturing
501 meta-information during ongoing digitization efforts at herbaria around the world and during
502 the accession of newly collected specimens (Edwards et al.; Lendemer et al., 2020). Second, we
503 accounted for several potential biases in the data observation process that may be common to
504 many collections-based research questions by using a spatially-explicit random effects model.
505 Spatial autocorrelation (Willems et al., 2022), potential biases introduced by the sampling habits
506 of collectors (Daru et al., 2018), and variation between contemporary researchers during the col-
507 lection of trait data, if not corrected for could lead to over-confident inference about the strength
508 and direction of historic change (Fig. 2). Previous studies that have quantified the effects of
509 collector biases typically find them to be small (Davis et al., 2015; Meineke et al., 2019), and we
510 similarly did not find that collector has a strong effect on the results of our analysis, but that
511 scorer identity did impact results.

512 Ultimately, a central goal of global change biology is to generate predictive insights into the
513 future of natural systems on a rapidly changing planet. Beyond host-microbe symbioses, de-
514 tecting ecological responses to anthropogenic global change and attributing their causes would
515 inform public policy decision-makers and adaptive management strategies. This survey of his-

516 toric endophyte prevalence is necessarily correlative, yet it serves as a foundation to develop
517 better predictive models of the response of microbial symbioses to climate change. By compar-
518 ing detected ecological responses with alternative mechanistic simulations of the past, we could
519 attribute their cause, in a manner similar to methods from climate science and economics (Car-
520 leton and Hsiang, 2016; Stott et al., 2010; Trenberth et al., 2015). Combining the insights from
521 this type of regional-scale survey with field experiments and physiological performance data
522 could be invaluable to identify mechanisms driving shifts in host-symbiont dynamics. Evidence
523 is strong that certain dimensions of climate change correlated with endophytes' temporal re-
524 sponses, however we do not know why trends in prevalence were weak in some areas or how
525 endophytes would respond to more extreme changes in climate. The "time machine" of natu-
526 ral history collections revealed evidence of mutualism resilience for grass-endophyte symbioses
527 in the face of environmental change, but more extreme changes could potentially push one or
528 both partners beyond their physiological limits, leading to the collapse of the mutualism; more
529 research is needed to understand what those limits might be.

530 **Acknowledgments**

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539

Statement of Authorship

540 J.C.F. contributed to research conception, data collection, data analysis, and led manuscript draft-
541 ing. J.M. contributed to data analysis and manuscript revisions. T.E.X.M. contributed to research
542 conception, data collection, data analysis, and manuscript revisions.

543

Data and Code Availability

544 Data from this publication can be found through a publicly available repository [\(\)](#)¹. Code for anal-
545 yses can be found through a publicly available repository (<https://github.com/joshuacfowler/EndoHerbarium>)
546 that will be permanently archived upon publication.

¹*will update with the URL*

Appendix A

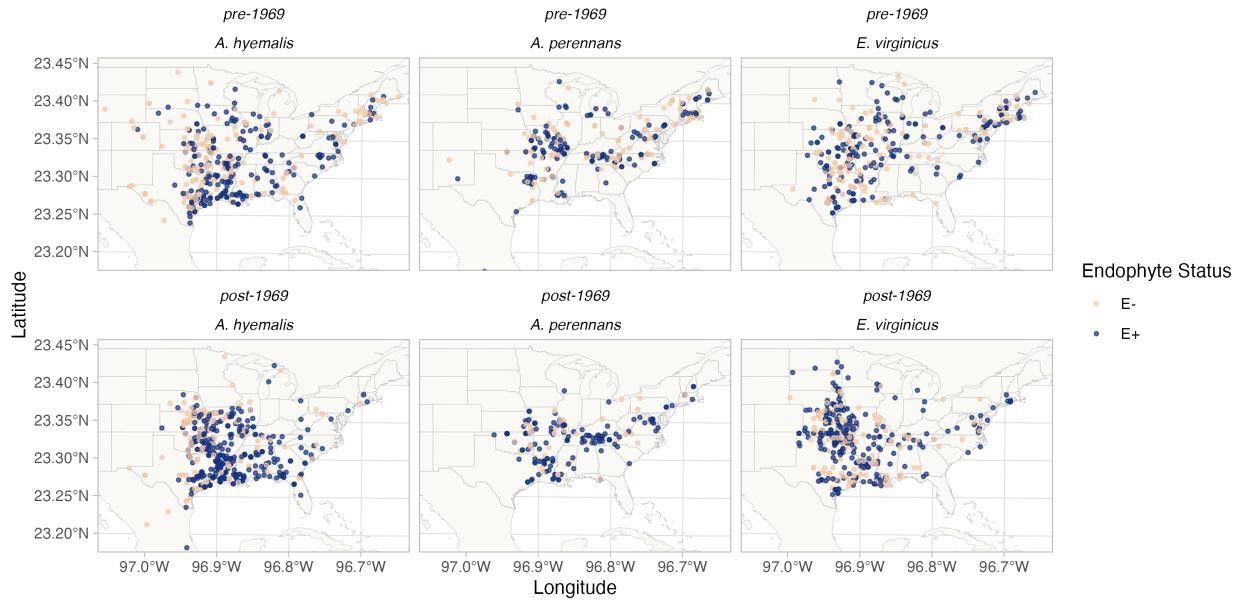


Figure A1: Endophyte presence/absence in specimens of each host species. Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points). To visualize temporal change, the data are faceted before and after the median year of collection.

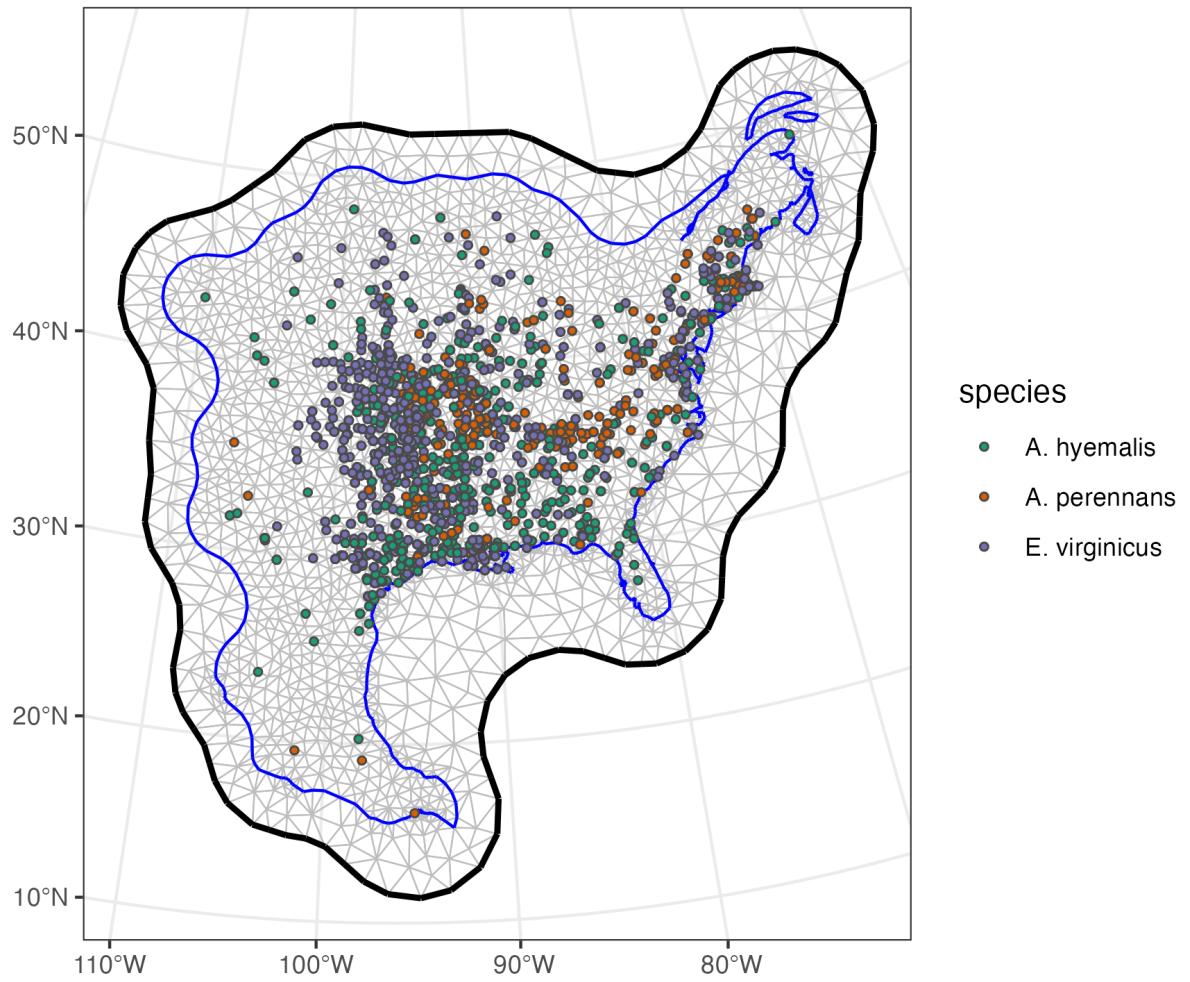


Figure A2: Triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull and coastline used to define the edge of the mesh around the data points. The thick black line shows the convex hull defining a buffer space around the edge of the mesh to reduce the influence of edge effects on model estimates.

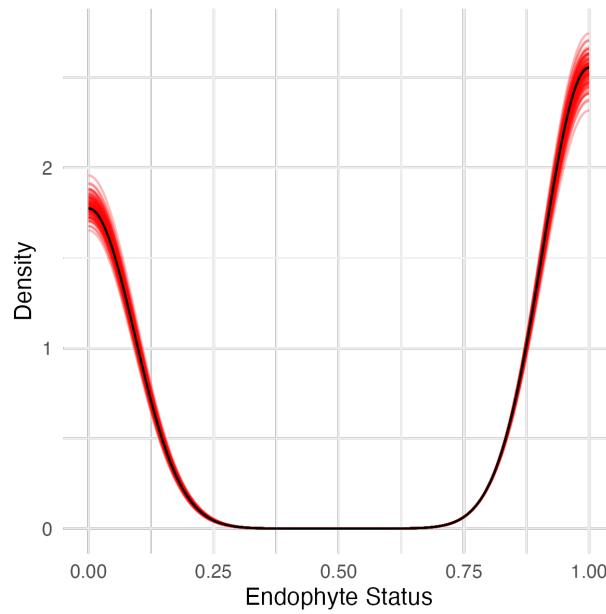


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (black) along with 100 simulated datasets (red).

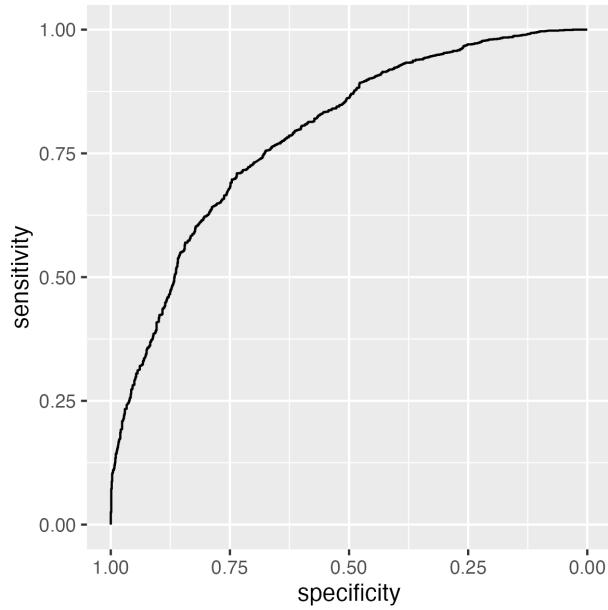


Figure A4: ROC plot showing model performance classifying observations according to endophyte status within the in-sample data. The curves show adequate model performance for observed data. The AUC value is 0.79.

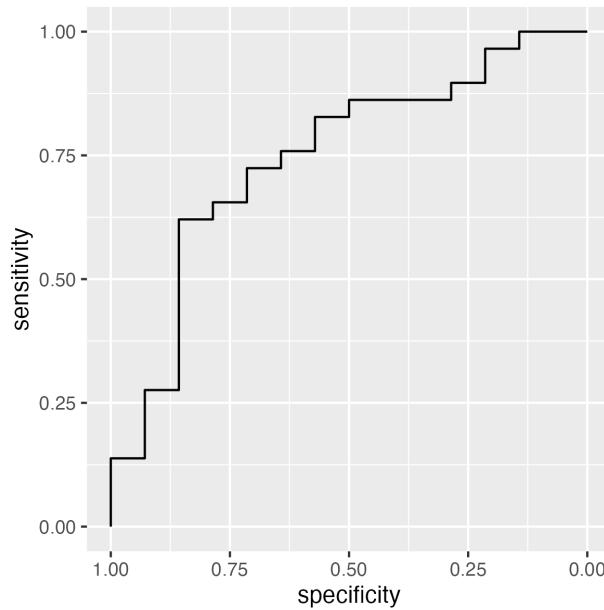


Figure A5: ROC plot showing model performance classifying observations according to endophyte status within the out-of-sample data. The curves show adequate model performance for test data. The AUC value is 0.77.

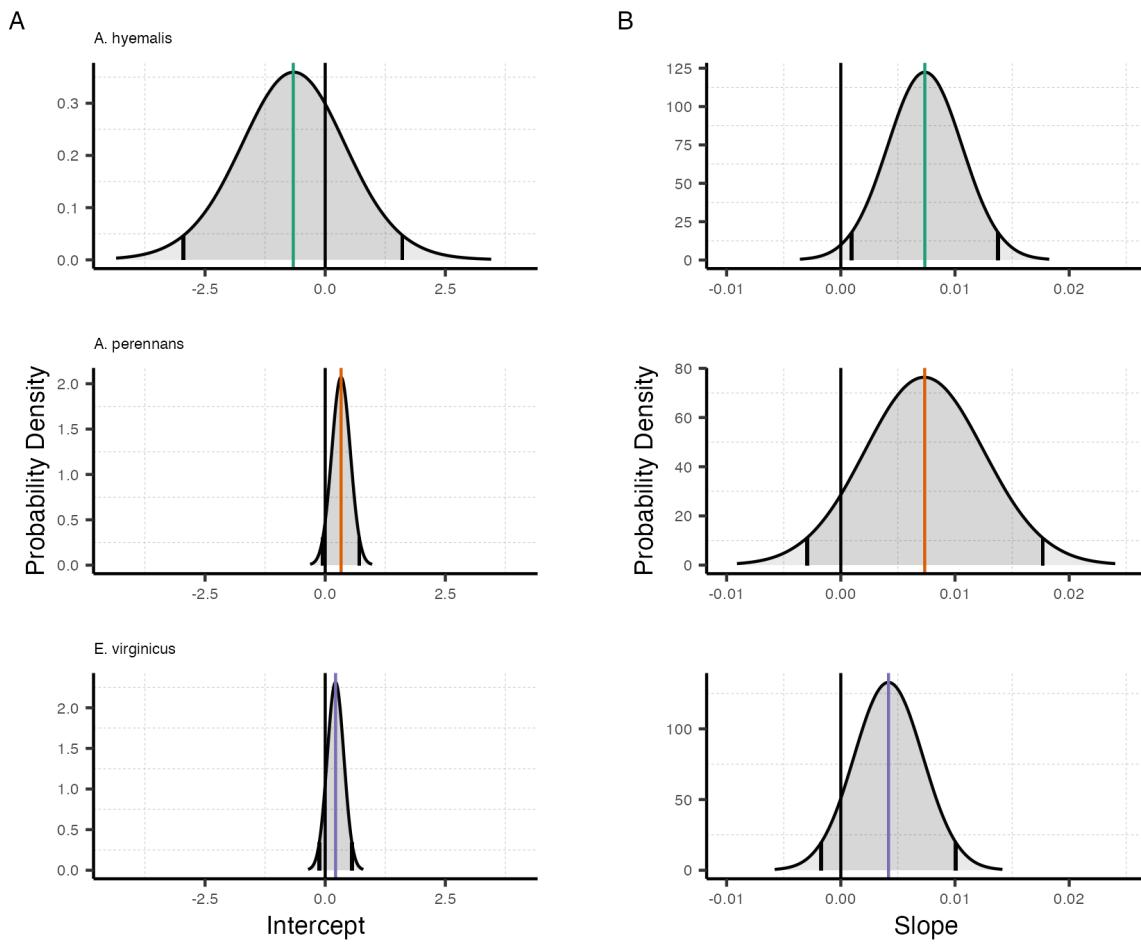


Figure A6: Density curves show the probability density along with mean (colored line) and 95% CI (black lines) for the (A) intercept and (B) slope terms, **A** and **T** respectively. Colors represent each host species

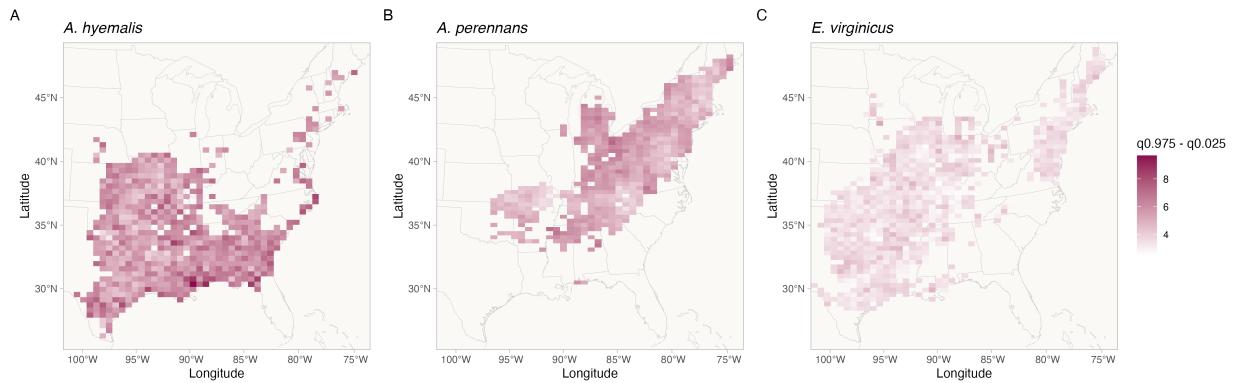


Figure A7: Shading represents the range of the 95% posterior credible interval for spatially varying slopes, τ .

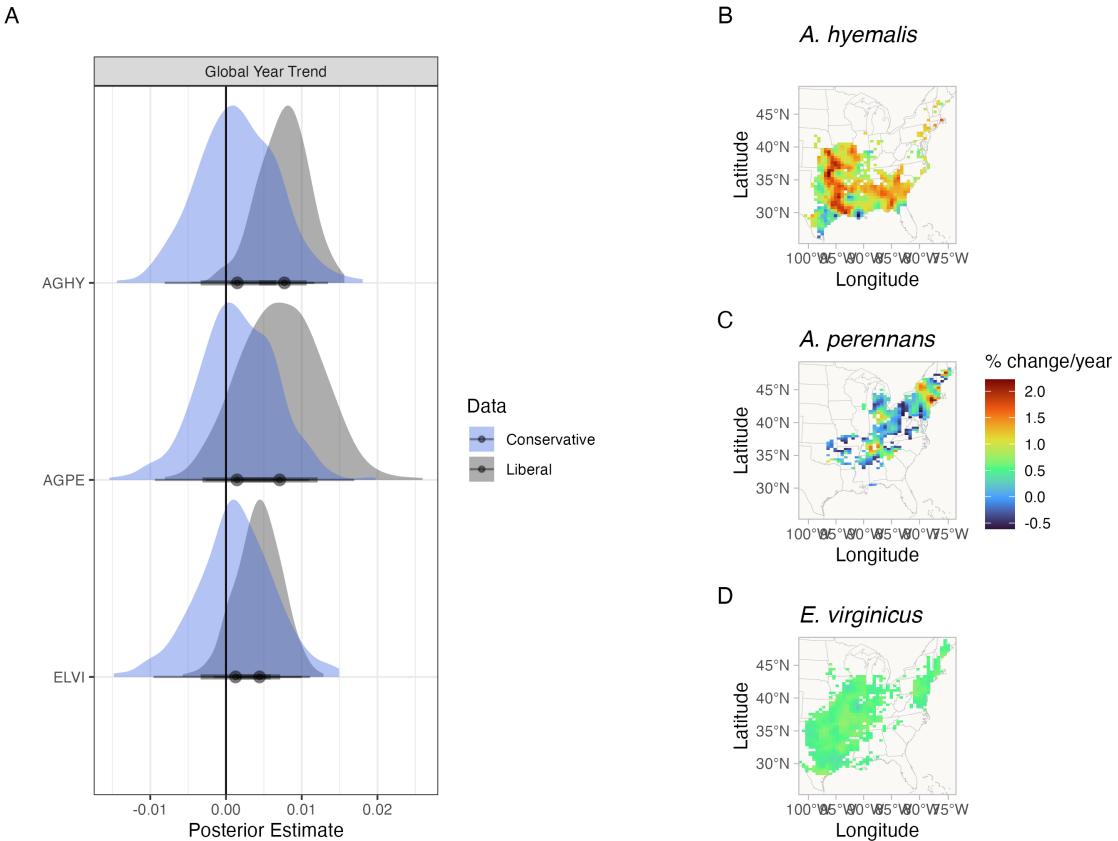


Figure A8: Comparison of liberal versus conservative endophyte scores on modeled outcomes. (A) Posterior estimates of global temporal trend for models fit to liberal scores (grey) and to conservative scores (blue). Maps show the spatially varying temporal trend estimates from model fit to conservative scores for (B) *A. hyemalis*, (C) *A. perennans*, and (D) *E. virginicus*. Note that the color scale differs between this visualization and Fig. 3.

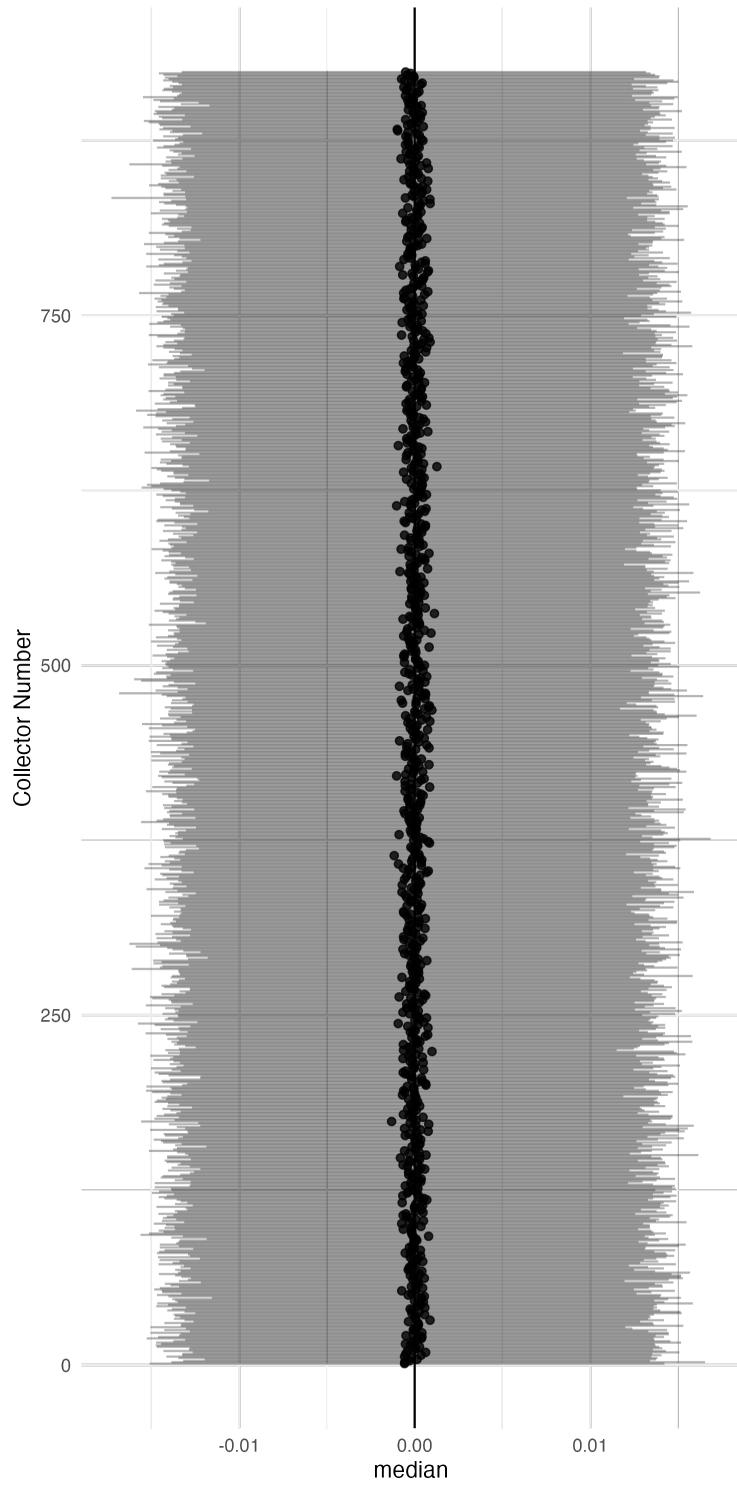


Figure A9: **Posterior estimates of collector random effects.** Points show posterior median along with 95% CI for each of 924 individual collectors.

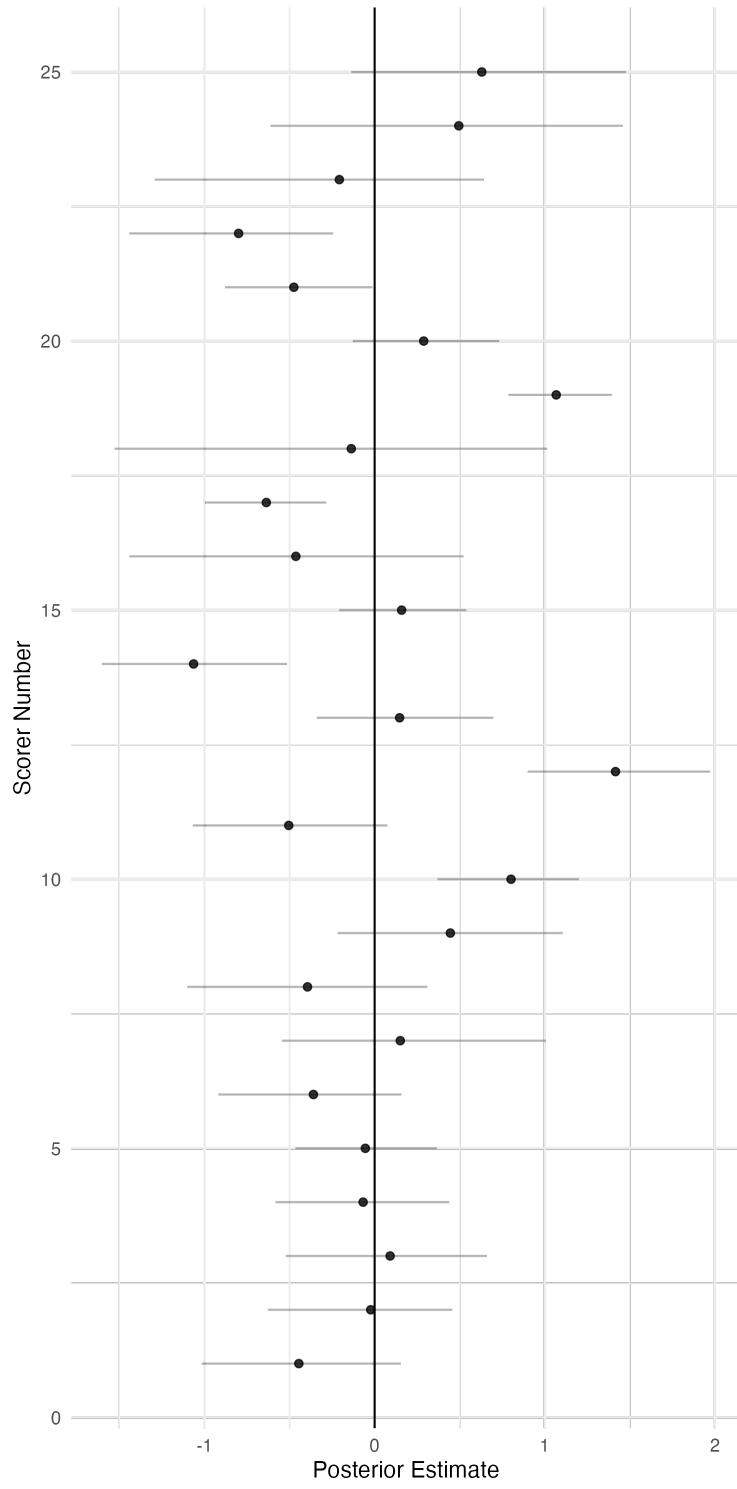


Figure A10: **Posterior estimates of scorer random effects.** Points show posterior median along with 95% CI for each of 25 individual collectors.

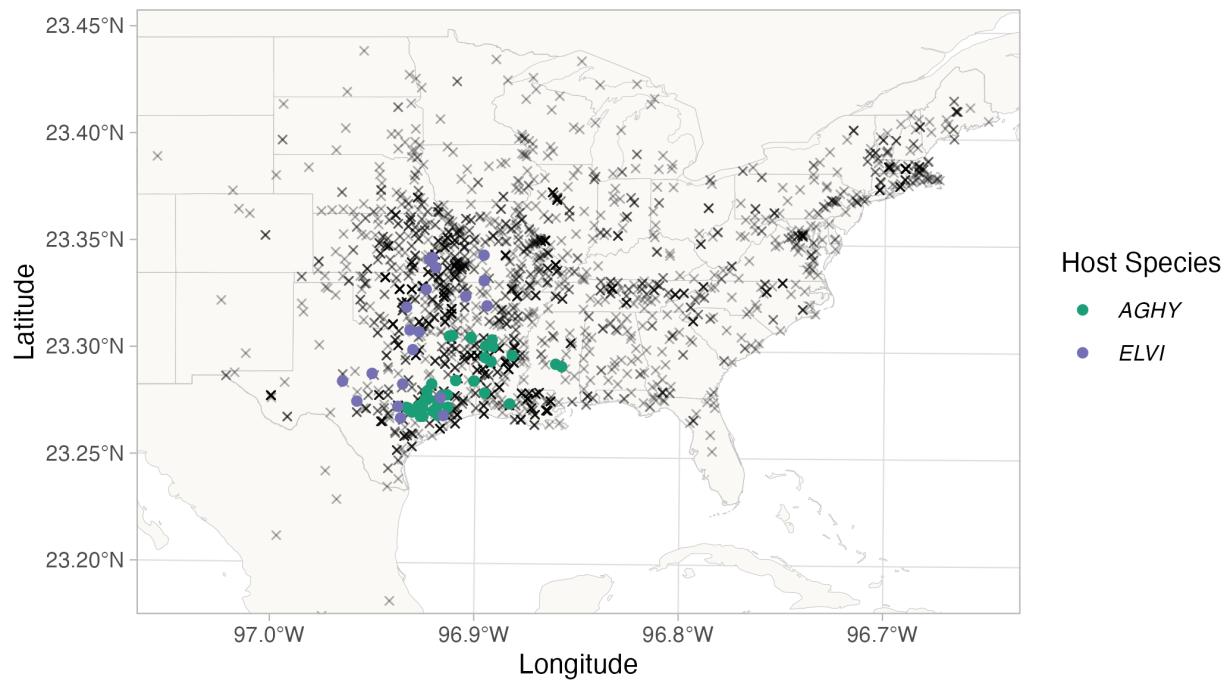


Figure A11: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

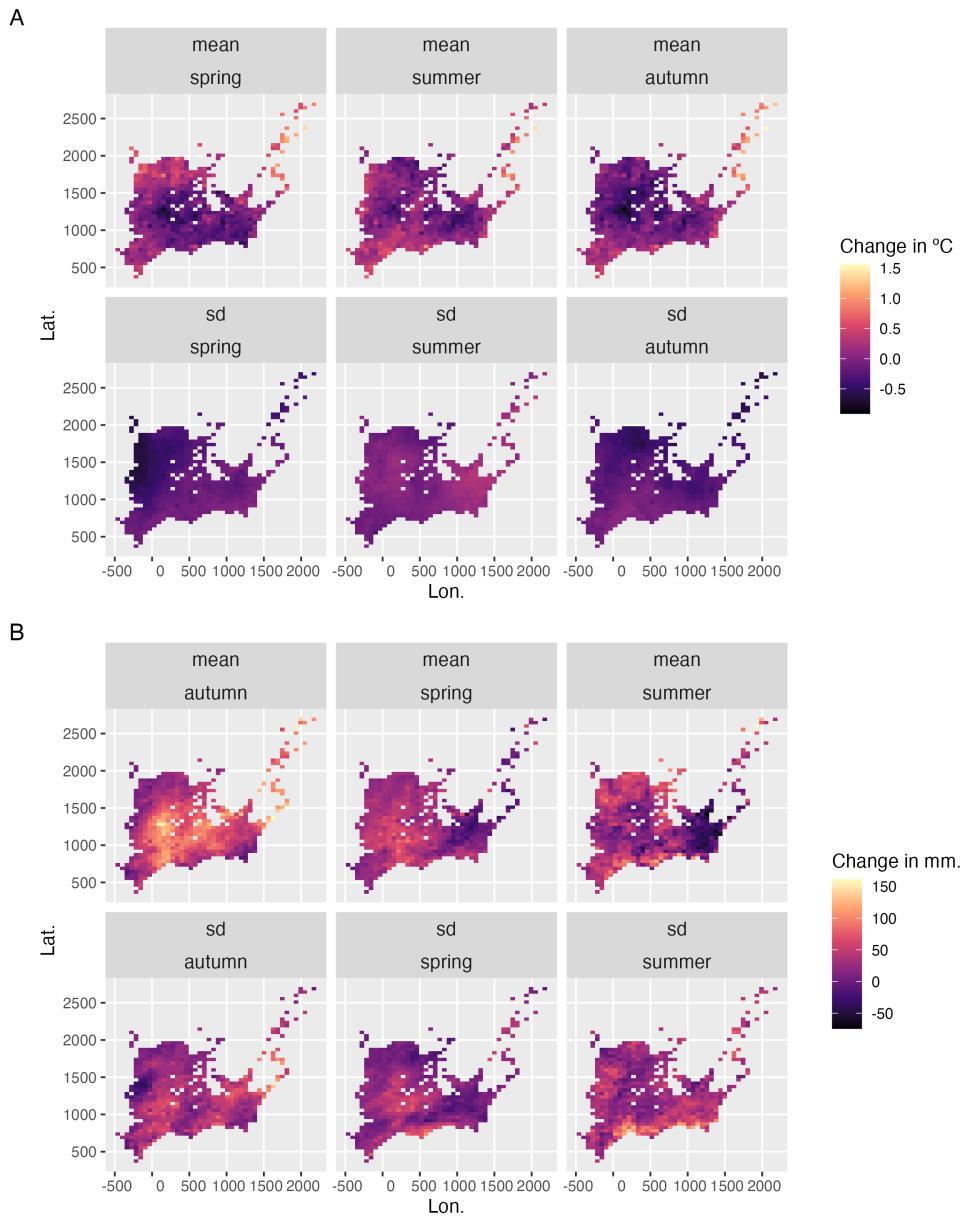


Figure A12: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. hyemalis* used in post-hoc climate correlation analysis.

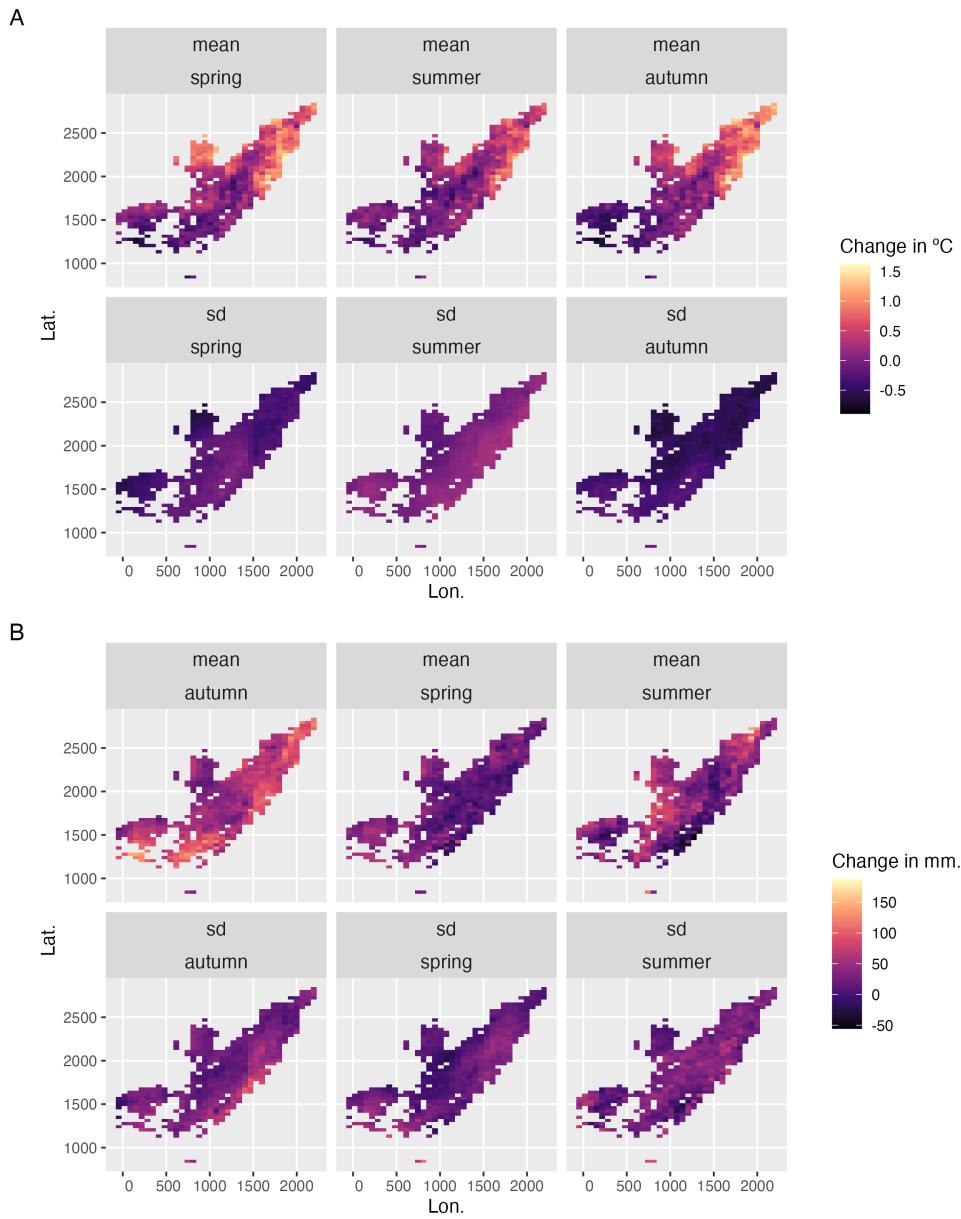


Figure A13: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020.

Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. perennans* used in post-hoc climate correlation analysis.

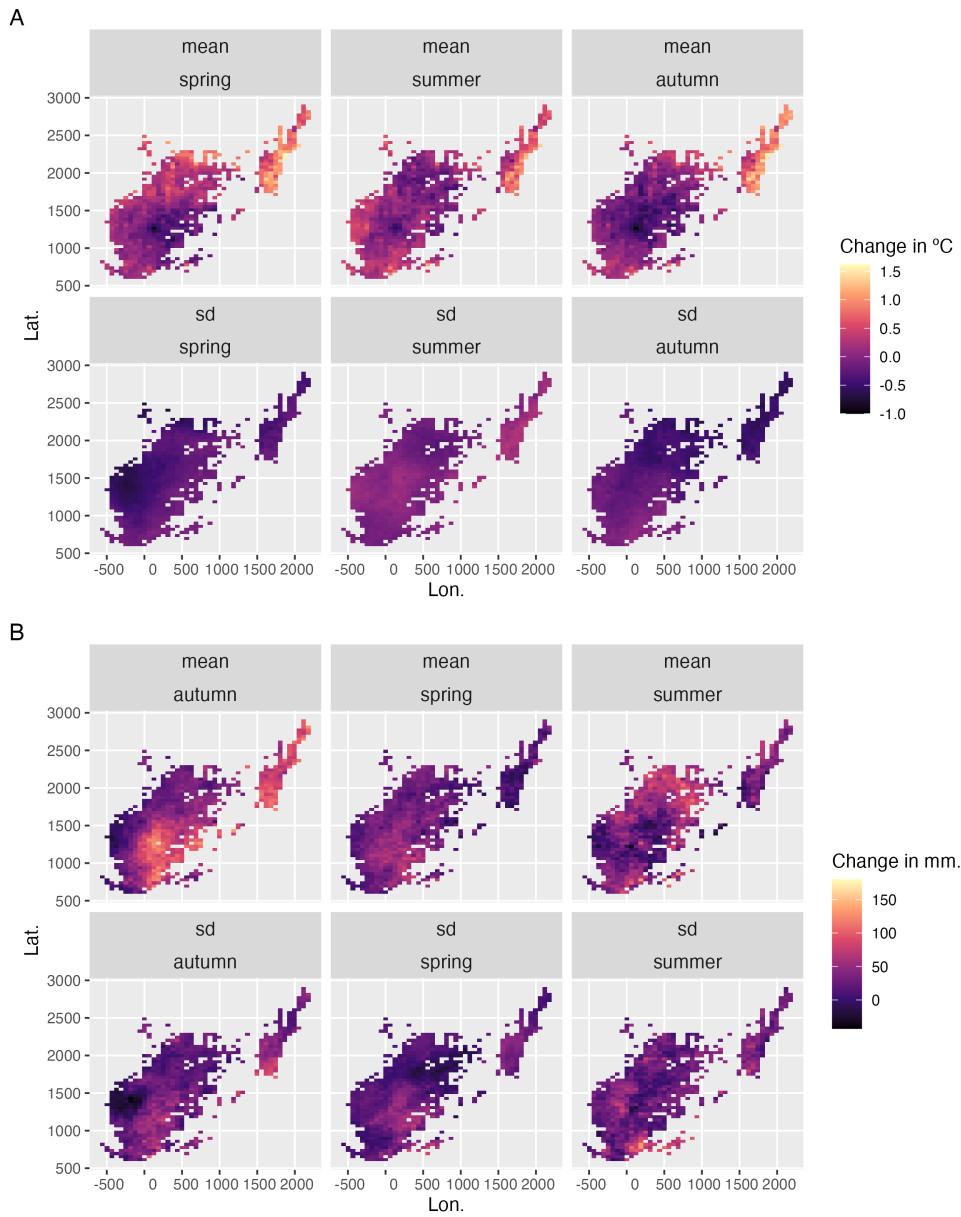


Figure A14: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *E. virginicus* used in post-hoc climate correlation analysis.

Table A1: Summary of herbarium samples across collections

Herbarium Collection	AGHY	AGPE	ELVI
Botanical Research Institute of Texas	350	190	198
Louisiana State University	72	38	62
Mercer Botanic Garden	3	–	6
Missouri Botanic Garden	210	205	122
Texas A&M	100	–	72
University of Kansas	134	34	197
University of Oklahoma	85	34	95
University of Texas & Lundell	183	91	102
Oklahoma State University	51	10	74

548

Supporting Methods

549

ODMAP Protocol

550 **Overview**

551 **Model purpose:** Mapping current distribution of *Epichloë* host species.

552 **Target species:** *Agrostis hyemalis*, *Agrostis perennans*, and *Elymus virginicus*.

553 **Study area:** Eastern North America

554 **Spatial extent:** -125.0208, -66.47917, 24.0625, 49.9375 (xmin, xmax, ymin, ymax).

555 **Spatial resolution:** 0.04166667, 0.04166667 (x, y).

556 **Temporal extent:** 1990 to 2020.

557 **Boundary:** Natural.

558 **Data**

559 **Observation type:** Occurrence records from Global Biodiversity Information Facility and herbar-

560 ium collection across eastern North America. We used 713 occurrences records for *Agrostis hye-*

561 *malis*, 656 occurrence records for *Agrostis perennans* and 2338 for *Elymus virginicus*.

562 **Response data type:** occurrence record, presence-only.

563 **Coordinate reference system:** WGS84 coordinate reference system (EPSG:4326 code)

564 **Climatic data:** raster data extracted from PRISM

565 **Model**

566 **Model assumption:** We assumed that the target species are at equilibrium with their environment.

568 **Algorithms:** Maximum entropy (maxent)

569 **Workflow:** We described the workflow in the method section of the manuscript.

570 **Software:** All statistics were performed using Maxent 3.3.4 and R4.3.1 with packages terra, usdm, spThin and dismo.

572 **Code availability:** Available through this link: <https://github.com/joshuacfowler/EndoHerbarium>

573 **Data availability:** Will be available upon acceptance

574 **Assessment**

575 We used AUC to test model performance.

576 **Prediction**

577 We predicted the probability of presence of the host species as a binary maps (presence or absence)

579 *Mesh and Prior Sensitivity analysis*

580 To test the influence that the triangulation mesh and choice of priors has on results, we compared
581 model results across a range of meshes and priors. We re-ran our model for the mesh used in
582 main body of the text (Fig. A2), which we refer to as the "standard mesh", and with a mesh with
583 smaller minimum vertices (finer mesh). Finer scale meshes increase computation time. For each
584 of these meshes, we ran the model with a range of priors defining the spatial range of our spatial
585 random effects: 342km (the prior used for presented results), as well as ranges five times smaller
586 (68 km) and five times larger (1714 km). We found generally that these choices did not alter the

587 direction of model predictions, but did influence the associated uncertainty and magnitude of
588 some effects.

589 For overall temporal trends, we found that models with differing priors predicted consistently
590 positive relationships over time (Fig. A15).

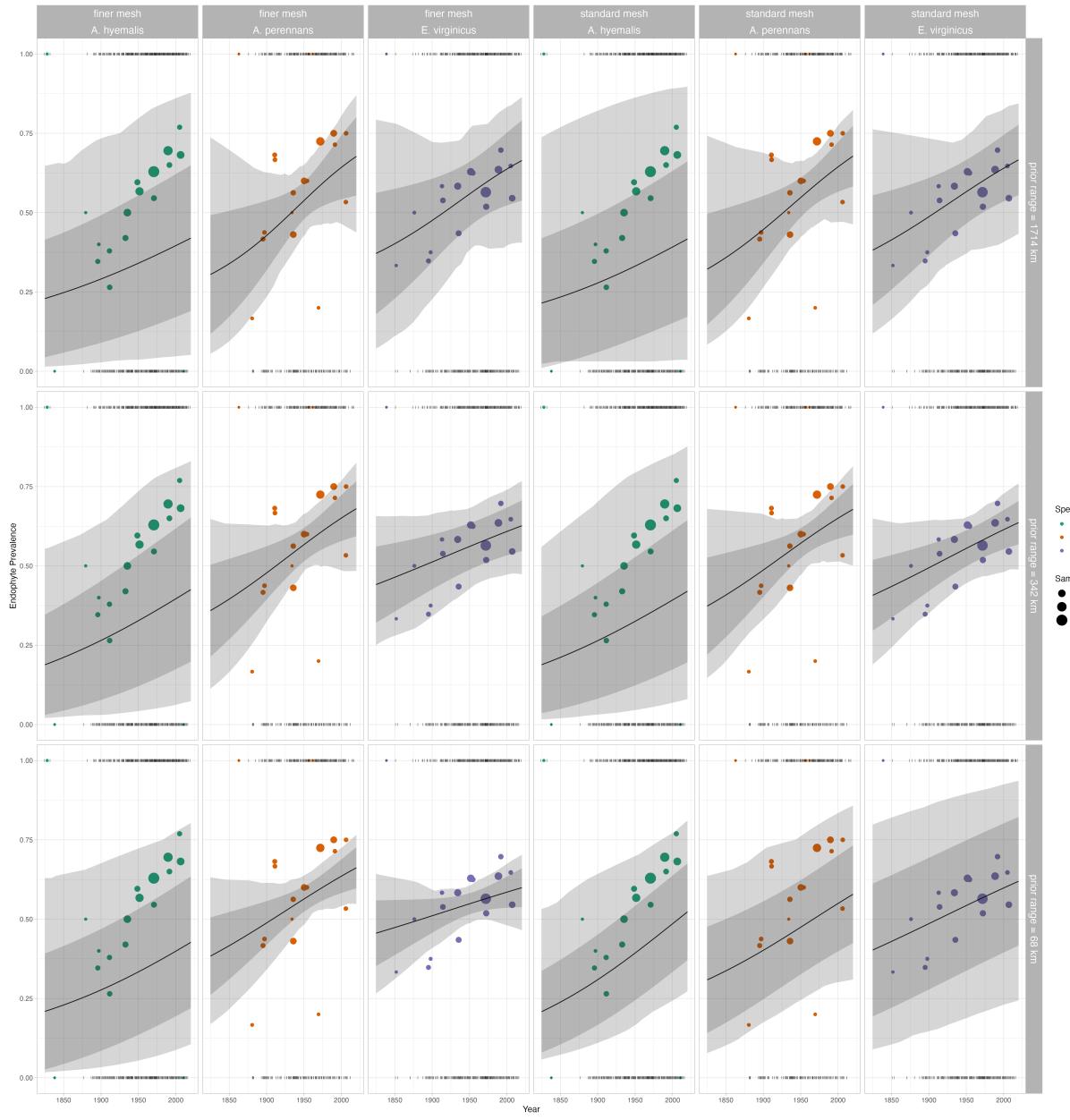


Figure A15: Overall trend in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for two different meshes. Note that these plots, as compared to Fig. 2 in main text, show mean trends and do not incorporate prediction uncertainty associated with collector and scorer random effects.

591 For spatially-varying temporal trends, we found that models with different priors predicted

592 consistent spatial patterns in temporal trends, although the range of this prediction varied de-
593 pending on the prior and mesh (Fig. A16 - A17). One noteworthy result of this analysis is that
594 combinations of prior choice and mesh can introduce instability in model fitting. This is evident
595 in A16 panel B and A17 panel B, where the prior range is smaller than the minimum vertex
596 length of the mesh. Model fitting takes an extended time period and the model struggles to
597 identify variation across space. Results with a set of prior ranges (Fig. A16 - A and C; Fig. A17
598 - A and C) result in models that estimate trends across space of the same direction and order of
599 magnitude, although the "smoothness" of these predictions vary.

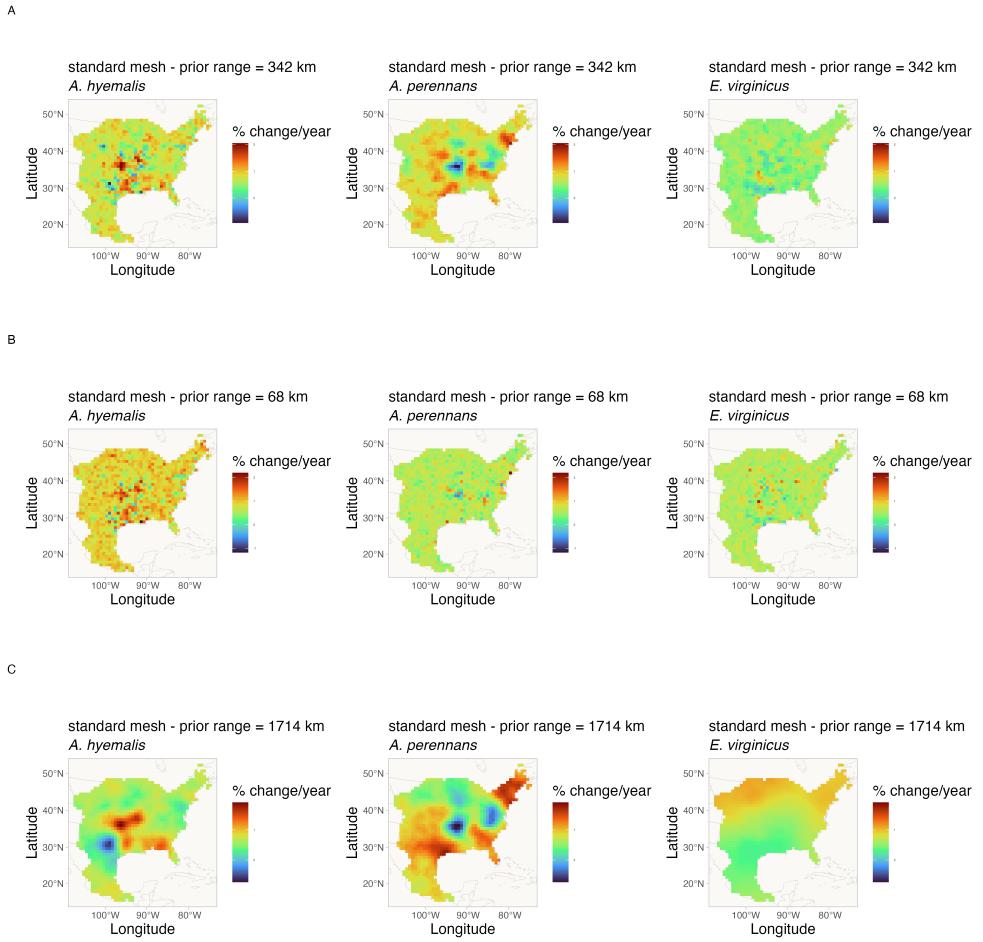
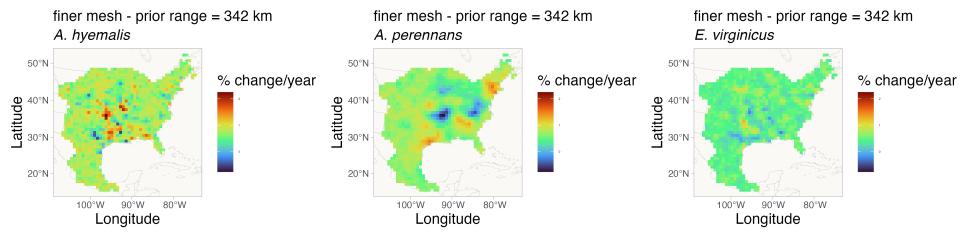
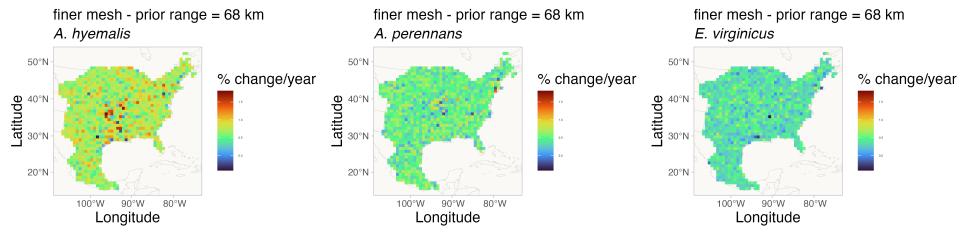


Figure A16: Spatially-varying trends in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for the "standard" mesh. Shading indicates the magnitude and direction of predicted trends for each of three host species for each of three prior ranges (rows A-C). Note that each plot has an individual scale bars.

A



B



C

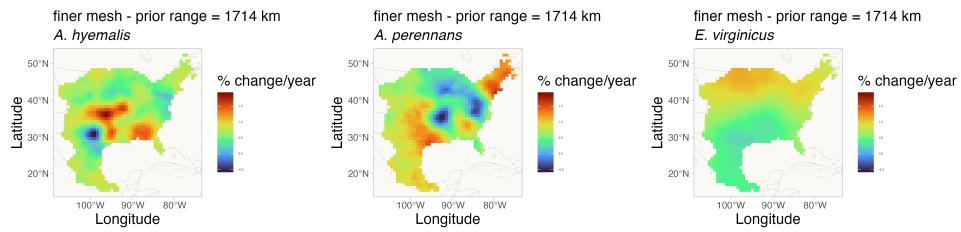


Figure A17: Spatially-varying trends in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for the "finer" mesh. Shading indicates the magnitude and direction of predicted trends for each of three host species for each of three prior ranges (rows A-C). Note that each plot has an individual scale bars.

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