

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

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Abstract

14 Species' distributions and abundances are shifting in response to ongoing global climate change.
15 Mutualistic microbial symbionts can provide hosts with protection from environmental stress
16 that may contribute towards resilience under environmental change, however this change may
17 also disrupt species interactions and lead to declines in hosts and/or symbionts. Symbionts
18 preserved within natural history specimens offer a unique opportunity to quantify changes in
19 microbial symbiosis across broad temporal and spatial scales. We asked how the prevalence
20 of seed-transmitted fungal symbionts of grasses (*Epichloë* endophytes) have changed over time
21 in response to climate change, and how these changes vary across host species' distributions.
22 Specifically, we examined 2,346 herbarium specimens of three grass host species (*Agrostis hye-*
23 *malis*, *Agrostis perennans*, *Elymus virginicus*) collected over the past two centuries (1824 – 2019) for
24 the presence or absence of *Epichloë* symbiosis. Analysis of an approximate Bayesian spatially-
25 varying coefficients model implemented in INLA revealed that endophytes increased in preva-
26 lence over the last two centuries from ca. 25% to ca. 75% prevalence, on average, across three host
27 species. Changes in seasonal climate drivers were associated with increasing endophyte preva-
28 lence. Notably, increasing precipitation during the peak growing season for *Agrostis* species and
29 decreasing precipitation for *E. virginicus* were associated with increasing endophyte prevalence.
30 Changes in the variability of precipitation and temperature during off-peak seasons were also
31 important predictors of increasing endophyte prevalence. Our analysis performed favorably in
32 an out-of-sample predictive test with contemporary survey data, a rare extra step in collections-
33 based research. However, we identified greater local-scale variability in endophyte prevalence
34 in contemporary data compared to model predictions based on historic data, suggesting new
35 directions that could improve predictive accuracy. Our results provide novel evidence for a cryp-
36 tic biological response to climate change that may contribute to the resilience of host-microbe
37 symbiosis through fitness benefits to symbiotic hosts.

38 Abstract : 300 words

Introduction

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

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

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

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

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

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

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

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

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

135 Methods

136 Focal species

137 Our surveys focused on three native North American grasses: *Agrostis hyemalis*, *Agrostis peren-*
138 *nans*, and *Elymus virginicus* that host *Epichloë* symbionts. These cool-season grass species are
139 commonly represented in natural history collections with broad distributions covering much the
140 eastern United States (Fig. 1). Cool-season grasses typically grow actively during the cooler tem-
141 peratures of spring and autumn due to their reliance on C₃ photosynthesis. *A. hyemalis* is a small
142 short-lived perennial species that germinates in spring and typically flowers between March and
143 July (most common collection month: May). *A. perennans* is of similar stature but is longer lived

¹⁴⁴ than *Agrostis hyemalis* and flowers in late summer and early autumn (most common collection
¹⁴⁵ month: September). *A. perennans* is more sparsely distributed, tending to be found in shadier
¹⁴⁶ and more moist habitats, while *A. hyemalis* is commonly found in open and recently disturbed
¹⁴⁷ ground. Both *Agrostis* species are recorded from throughout the Eastern US, but *A. perennans* has
¹⁴⁸ a slightly more northern distribution, whereas *A. hyemalis* is found rarely as far north as Canada
¹⁴⁹ and is listed as a rare plant in Minnesota. *E. virginicus* is a larger and relatively longer-lived
¹⁵⁰ species that is more broadly distributed than the *Agrostis* species. It begins flowering as early as
¹⁵¹ March or April but continues throughout the summer (most common collection month: July).

¹⁵² Both *Agrostis* species host *Epichloë amarillans* (Craven et al., 2001; Leuchtmann et al., 2014),
¹⁵³ while *Elymus virginicus* typically hosts *Epichloë elymi* (Clay and Schardl, 2002). The fungal sym-
¹⁵⁴ bionts primarily reproduce asexually and are passed from mother to offspring by vertical trans-
¹⁵⁵ mission through seeds. These traits contribute to highly specialized interactions between sym-
¹⁵⁶ biont and host. Some host species have been shown to partner with multiple symbiont species
¹⁵⁷ in these genus, and in some cases multiple symbiont species can co-exist within a host popu-
¹⁵⁸ lation (Mc Cargo et al., 2014). However, suveys have typically found limited *Epichloë* genotypic
¹⁵⁹ diversity within host populations(Treindl et al., 2023). Across host populations, concentrations
¹⁶⁰ of biologically-active alkaloids and the genes associated with their production vary substantially
¹⁶¹ (Schardl et al., 2012).

¹⁶² *Herbarium surveys*

¹⁶³ We visited nine herbaria between 2019 and 2022 (see Table A1 for a summary of specimens in-
¹⁶⁴ cluded from each collection). With permission from herbarium staff, we acquired seed samples
¹⁶⁵ from 1135 *A. hyemalis* specimens collected between 1824 and 2019, 357 *A. perennans* specimens
¹⁶⁶ collected between 1863 and 2017, and 854 *E. virginicus* specimens collected between 1839 and
¹⁶⁷ 2019 (Fig. 1, Fig. 2A, Fig. A1). We chose our focal species in part because they are commonly
¹⁶⁸ represented in herbarium collections, and produce high numbers of seeds, meaning that small
¹⁶⁹ samples would not diminish the value of the specimens for future studies. We collected up

170 to 5-10 seeds per specimen after examining the herbarium sheet under a dissecting microscope
171 to ensure that we collected mature seeds, not florets or unfilled seeds, fit for our purpose of
172 identifying fungal endophytes with microscopy. We excluded specimens for which information
173 about the collection location and date were unavailable. Each specimen was assigned geographic
174 coordinates based on collection information recorded on the herbarium sheet using the geocod-
175 ing functionality of the ggmap R package (Kahle et al., 2019). Many specimens had digitized
176 collection information readily available, but for those that did not, we transcribed information
177 printed on the herbarium sheet. Collections were geo-referenced to the nearest county centroid,
178 or nearest municipality when that information was available. For fifteen of the oldest specimens,
179 only information at the state level was available, and so we used the state centroid.

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

197 conservative status which yielded qualitatively similar results (Fig. A8).

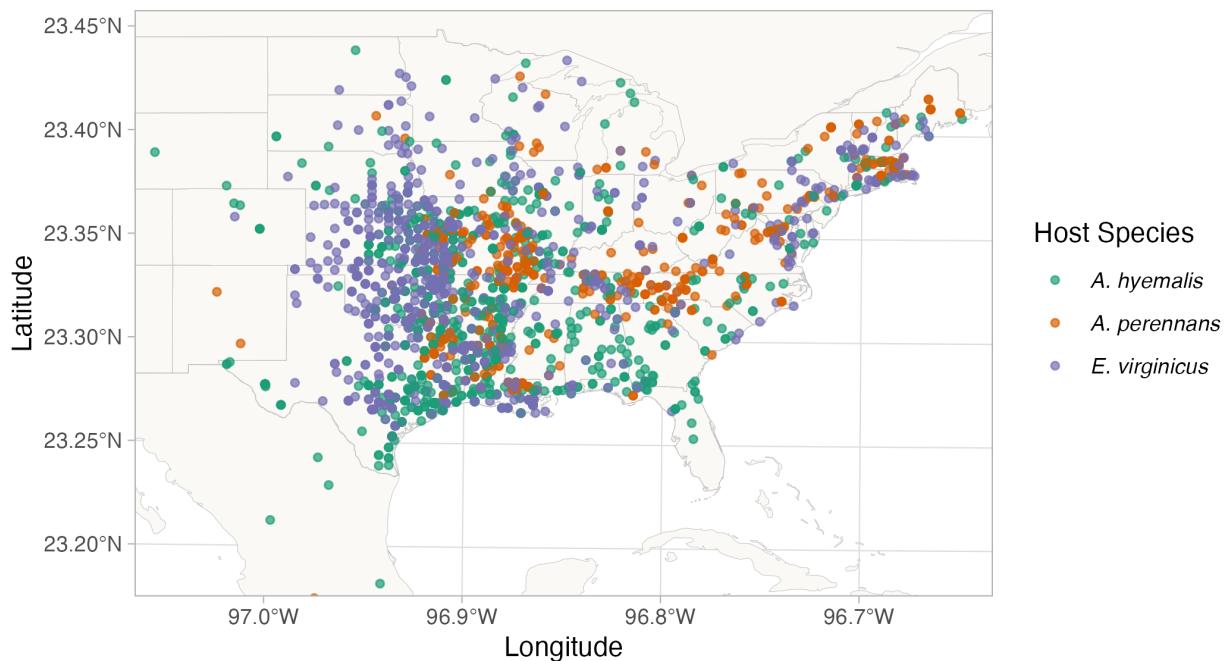


Figure 1: Collection locations of herbarium specimens sampled for *Epichloë* endophytes. Specimens span eastern North America from nine herbaria, and are colored by host species.

198 Modeling spatial and temporal changes in endophyte prevalence

199 We assessed spatial and temporal changes in endophyte prevalence across each host distribution,
200 quantifying the “global” temporal trends aggregated across space, and then examining spatial
201 heterogeneity in the direction and magnitude of endophyte change (hotspots and coldspots)
202 across the spatial extent of each host’s distribution. To account for the spatial non-independence
203 of geo-referenced occurrences, we used an approximate Bayesian method, Integrated Nested
204 Laplace Approximation (INLA), to construct spatio-temporal models of endophyte prevalence.
205 INLA provides a computationally efficient method of ascertaining parameter posterior distribu-
206 tions for certain models that can be formulated as latent Gaussian Models (Rue et al., 2009).
207 Many common statistical models, including structured and unstructured mixed-effects models,

208 can be represented as latent Gaussian Models. We incorporated spatial heterogeneity into this
 209 analysis using spatially-structured intercept and slope parameters implemented as stochastic
 210 partial differential equations (SPDE) to approximate a continuous spatial Gaussian process. This
 211 SPDE approach is a flexible method of smoothing across space while explicitly accounting for
 212 spatial dependence between data-points (Bakka et al., 2018; Lindgren et al., 2011). Fitting models
 213 with structured spatial effects is possible with MCMC sampling but can require long computa-
 214 tion times, making INLA an effective alternative. This approach has been used to model spatial
 215 patterns in flowering phenology (Willems et al., 2022), the abundance of birds (Meehan et al.,
 216 2019) and butterflies (Crossley et al., 2022), the distribution of temperate trees (Engel et al., 2022)
 217 as well as the population dynamics of endangered amphibians (Knapp et al., 2016) and other
 218 ecological processes (Beguin et al., 2012).

219 We estimated global and spatially-varying trends in endophyte prevalence using a joint-
 220 likelihood model. For each host species h , endophyte presence/absence of the i^{th} specimen ($P_{h,i}$)
 221 was modeled as a Bernoulli response variable with expected probability of endophyte occurrence
 222 $\hat{P}_{h,i}$. We modeled $\hat{P}_{h,i}$ as a linear function of intercept A_h and slope T_h defining the global trend
 223 in endophyte prevalence specific to each host species as well as with spatially-varying intercepts
 224 α_{h,l_i} and slopes τ_{h,l_i} associated with location (l_i , the unique latitude-longitude combination of the
 225 i^{th} observation). The joint-model structure allowed us to “borrow strength” across species in
 226 the estimation of shared variance terms for the spatially-dependent random effect δ_{l_i} , intended
 227 to account for residual spatial variation, and χ_{c_i} and ω_{s_i} i.i.d.-random effects indexed for each
 228 collector identity (c_i), and scorer identity (s_i) of the i^{th} specimen.

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

229 By including random effects for collectors and scorers, we accounted for “nuisance” variance
 230 that may bias predictions for changes in endophyte prevalence. Previous work suggests that
 231 behavior of historical botanists may introduce biases into ecological inferences made from historic
 232 collections (Kozlov et al., 2020). Prolific collectors who contribute thousands of specimens may

233 be more or less likely to collect certain species, or specimens with certain traits (Daru et al., 2018).
234 Similarly, the process of scoring seeds for hyphae involved several student researchers who, even
235 with standardized training, may vary in their likelihood of positively identifying *Epichloë*.

236 We performed model fitting using the inlabru R package (Bachl et al., 2019). Global intercept
237 and slope parameters A , and T , were given vague priors. Scorer and collector random effects,
238 χ and ω , were given penalized complexity priors, with distributions approximating a Normal
239 distribution with standard deviation of 5. Each spatially-structured parameter depended on a
240 covariance matrix according to the proximity of each pair of collection locations (Bakka et al.,
241 2018; Lindgren et al., 2011). The covariance matrix was approximated using a Matérn covariance
242 function, with each data point assigned a location according to the nodes of a mesh of non-
243 overlapping triangles encompassing the study area (Fig. A2). We assessed model fit with visual
244 posterior predictive checks (A3) and measurements of AUC (Figs. A4-A5). Priors for the Matérn
245 covariance function, termed "range" and "variance", define how proximity effects decay with
246 distance. Results presented in the main text reflect a prior range of 342 kilometers (i.e. a 50%
247 probability of estimating a range less than 342 kilometers). We tested a range of values (from 68
248 kilometers to 1714 kilometers) and meshes (presented in the Supporting Methods), finding that
249 while the magnitude and uncertainty of effects varied, model results were qualitatively similar,
250 i.e. the same direction of effects across space.

251 *Modeling distributions of host species*

252 Because the herbarium records did not encompass the entirety of these host species' ranges,
253 we additionally modeled the geographic distribution of each host species to generate realistic
254 maps on which we could project the predictions of the INLA model. We followed the ODMAP
255 (overview, data, model, assessment, prediction) protocol (Crossley et al., 2022) (see Supporting
256 Methods). In short, we used presence-only observations of each host species from Global Bio-
257 diversity Information Facility (GBIF) between 1990 to 2020. We fit maximum entropy (MaxEnt)
258 models using the maxent function in the R package dismo (Hijmans et al., 2017) using the same

259 set of seasonal climate predictors considered above calculated for the 1990-2020 climate normals:
260 mean and standard deviation of spring, summer, and autumn temperature, and mean and stan-
261 dard deviation of spring, summer, and autumn cumulative precipitation. We generated 10,000
262 pseudo-absences as background points, and split the occurrence data into 75% for model train-
263 ing and 25% for model testing. The performance of models was evaluated with AUC (Jiménez-
264 Valverde, 2012). We found AUC values of 0.862, 0.838, 0.821 respectively for *Agrostis hyemalis*,
265 *Agrostis perennans*, and *Elymus virginicus* indicating good model fit to data. To convert the contin-
266 uous predicted probabilities into binary presence - absence maps on which we projected INLA
267 predictions, we used the training sensitivity (true positive rate) and specificity threshold (true
268 negative rate) (Liu et al., 2005).

269 *Assessing the role of climate drivers*

270 We assessed how the magnitude of climate change may have driven changes in endophyte preva-
271 lence by assessing correlations between changes in climate and changes in endophyte prevalence
272 predicted from our spatial model at evenly spaced pixels across the study area. We first down-
273 loaded monthly temperature and precipitation rasters from the PRISM climate group (Daly and
274 Bryant, 2013) covering the time period between 1895 and 2020 using the 'prism' R package (Hart
275 and Bell, 2015). Prism provides reconstructions of historic climate variables across the United
276 States by spatially-interpolating weather station data (Di Luzio et al., 2008). We calculated 30-
277 year climate normals for seasonal mean temperature and cumulative precipitation for the recent
278 (1990 to 2020) and historic (1895 to 1925) periods. We used three four-month seasons within
279 the year (Spring: January, February, March, April; Summer: May, June, July, August; Autumn:
280 September, October, November, December). This division of seasons allowed us to quantify dif-
281 ferences in climate associated with the two "cool" seasons, when we expected our focal species
282 to be most biologically active (*A. hyemalis* flowering phenology: spring; *E. virginicus*: spring and
283 summer; *A. perennans*: autumn). In addition to mean climate conditions, environmental vari-
284 ability itself can influence population dynamics (Tuljapurkar, 1982) and changes in variability

are a key prediction of climate change models (IPCC, 2021; Stocker et al., 2013). Therefore, we calculated the standard deviation for each annual and seasonal climate driver across each 30-year period. We then took the difference between recent and historic periods for the mean and standard deviation for each climate driver (Figs. A12-A14). All together, we assessed twelve potential climate drivers: the mean and standard deviation of spring, summer, and autumn temperature, as well as the mean and standard deviation of spring, summer, and autumn cumulative precipitation.

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

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

We evaluated the predictive ability of the model using both in-sample training data from the herbarium surveys, and with out-of-sample test data, an important but rarely used strategy in ecological studies (Lee et al., 2024; Tredennick et al., 2021). We generated out-of-sample test data from contemporary surveys of endophyte prevalence in natural populations of *A. hyemalis* and *E. virginicus* in Texas and the southern US. Surveys of *E. virginicus* were conducted in 2013 as described in Sneck et al. (2017), and surveys of *A. hyemalis* took place between 2015 and 2020. Population surveys of *A. hyemalis* were initially designed to cover longitudinal variation in endophyte prevalence towards its range edge, while surveys of *E. virginicus* were designed to cover latitudinal variation. In total, we visited 43 populations of *A. hyemalis* and 20 populations of *E. virginicus* across the south-central US, with emphasis on Texas and neighboring states (Fig

311 A11). During surveys, we collected seeds from up to 30 individuals per population (average
312 number of plants sampled per population: 22.9); note that this sampling design provided greater
313 local depth of information than the herbarium records, where only one plant was sampled at
314 each locality. We quantified the endophyte status of each individual with staining microscopy
315 as described for the herbarium surveys (with 5-10 seeds scored per individual), and calculated
316 the prevalence of endophytes within the population (proportion of plants that were endophyte-
317 symbiotic). For each population, we compared the observed fraction of endophyte-symbiotic
318 hosts to the predicted probability of endophyte occurrence \hat{P} derived from the model for that
319 location and year. The contemporary survey period (2013-2020) is at the most recent edge of the
320 time period encompassed by the historical observations used for model fitting.

321 **Results**

322 *How has endophyte prevalence changed over time?*

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

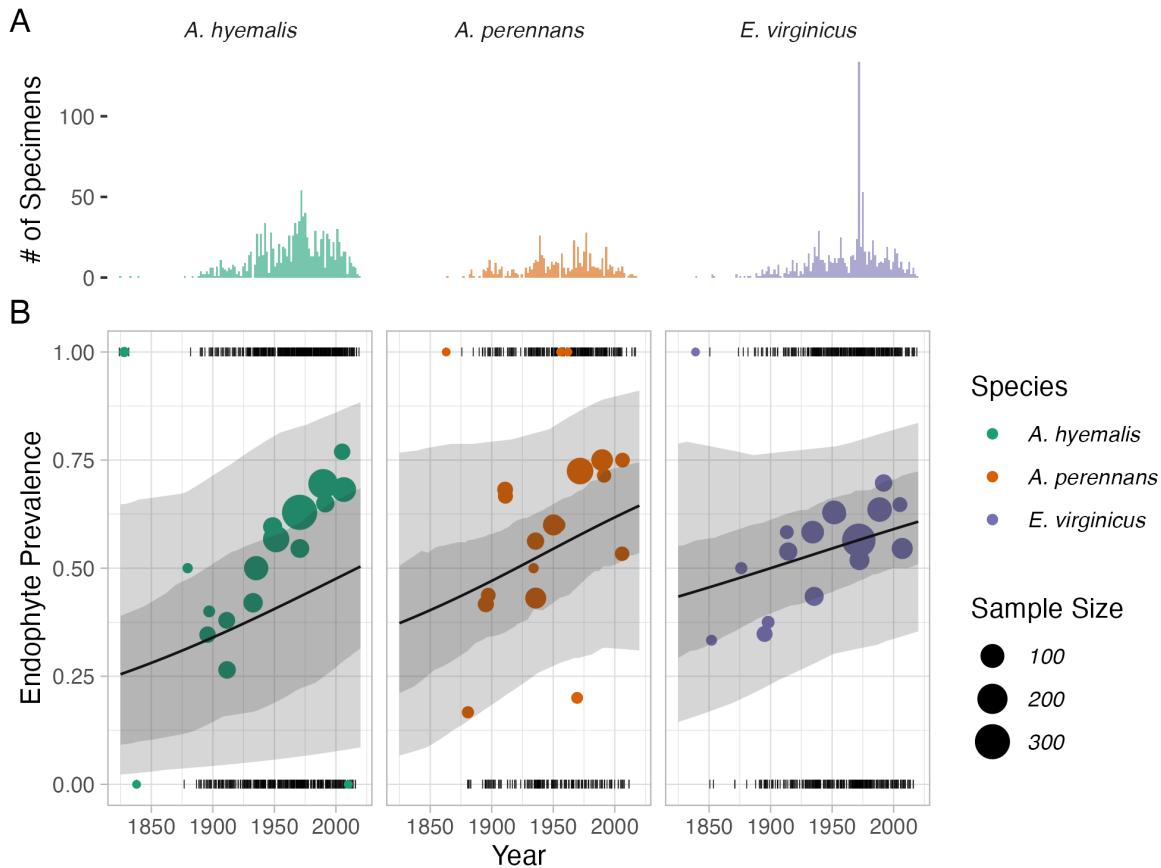


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of scored specimens through time for each host species. (B) Lines show predicted mean endophyte prevalence over the study period along with the 50% and 95% CI bands incorporating uncertainty associated with collector 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.

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

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

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

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

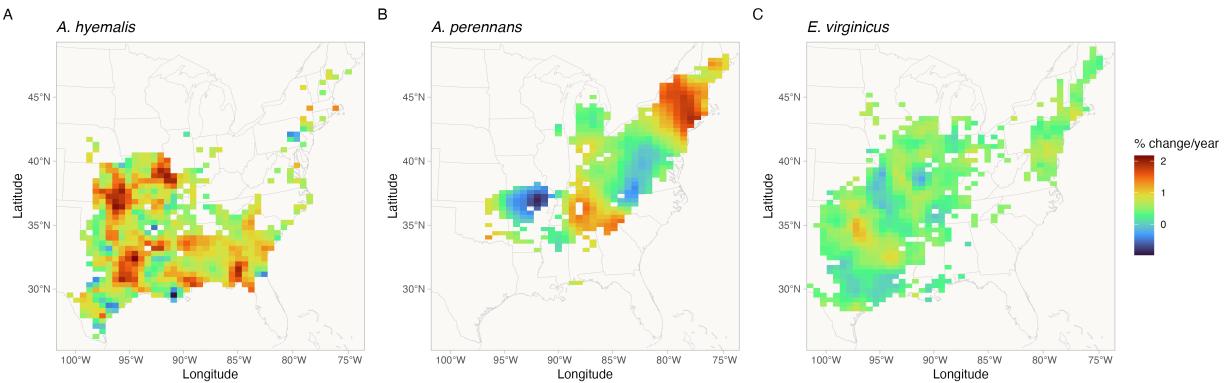


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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.

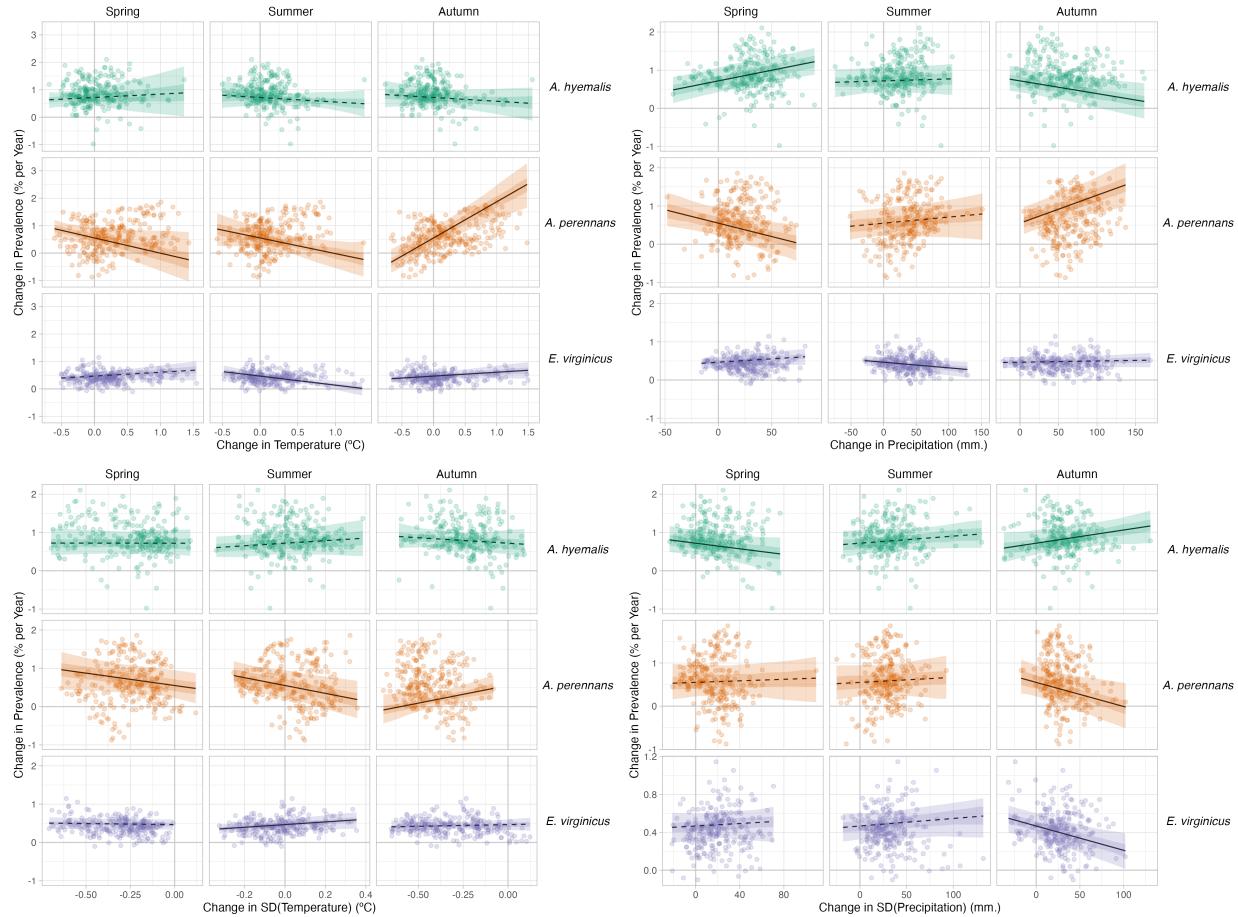


Figure 4: Relationships between predicted trends in endophyte prevalence and changes in seasonal climate drivers. Lines show marginal predicted relationship between spatially-varying trends in endophyte prevalence and changes in mean and variability of climate ((A): mean temperature, (B): cumulative 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.

398 *Performance on test data*

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

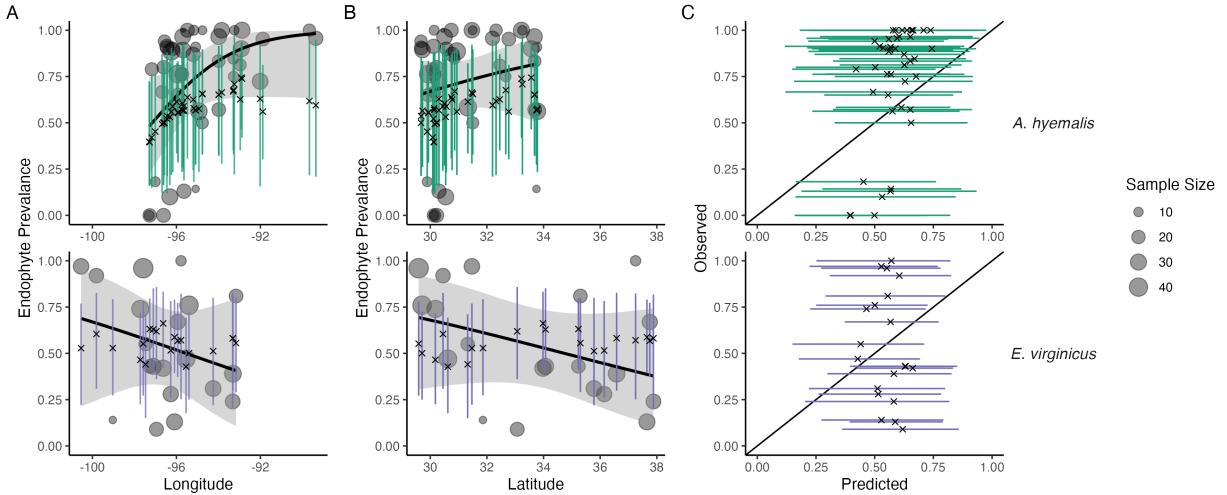


Figure 5: Predictive performance for contemporary test data. (A) The model, trained on historic herbarium collection data, performed modestly at predicting prevalence in contemporary population surveys. The model captured regional trends across (A) longitude and (B) latitude. Crosses indicate predicted 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

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

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

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

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

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

490 Our analysis advances the use of herbarium specimens in global change biology in two ways.
491 First and foremost, this is one of a growing number of studies to examine microbial symbiosis us-
492 ing specimens from natural history collections, and the first, to our knowledge, to link long-term
493 changes in the symbioses to changes in climate. The responses of microbial symbioses are a rich
494 target for future studies within museum specimens, particularly those that take advantage of ad-
495 vances in sequencing technology. While we used relatively coarse presence/absence data based
496 on fungal morphology, other studies have examined historic plant microbiomes using molecu-
497 lar sequencing and sophisticated bioinformatics techniques, but these studies have so far been
498 limited to relatively few specimens at limited spatial extents (Bieker et al., 2020; Bradshaw et al.,

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

523 Ultimately, a central goal of global change biology is to generate predictive insights into the
524 future of natural systems on a rapidly changing planet. Beyond host-microbe symbioses, de-
525 tecting ecological responses to anthropogenic global change and attributing their causes would

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

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550

Statement of Authorship

551 J.C.F. contributed to research conception, data collection, data analysis, and led manuscript draft-
552 ing. J.M. contributed to data analysis and manuscript revisions. T.E.X.M. contributed to research
553 conception, data collection, data analysis, and manuscript revisions.

554

Data and Code Availability

555 Data from this publication can be found through a publicly available repository
556 (<https://doi.org/10.5061/dryad.rn8pk0pn0>). Code for analyses can be found through a pub-
557 licly available repository (<https://github.com/joshuacfowler/EndoHerbarium>) that will be per-
558 manently archived upon publication.

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Appendix A

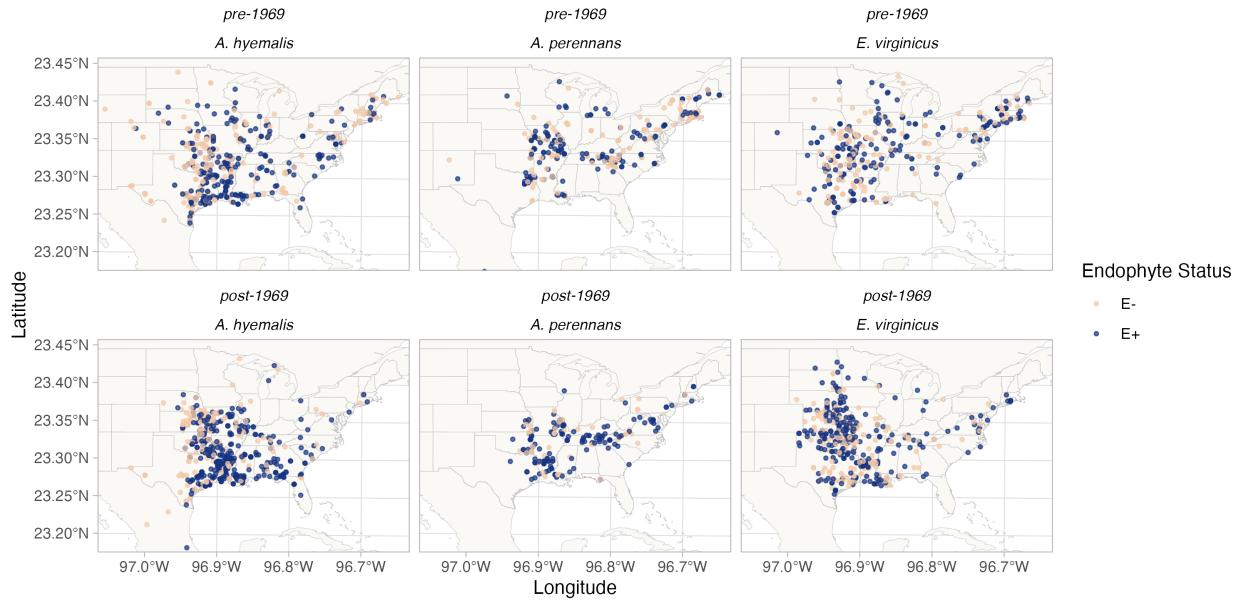


Figure A1: Endophyte presence/absence in specimens of each host species. Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points). To visualize temporal change, the data are faceted before and after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

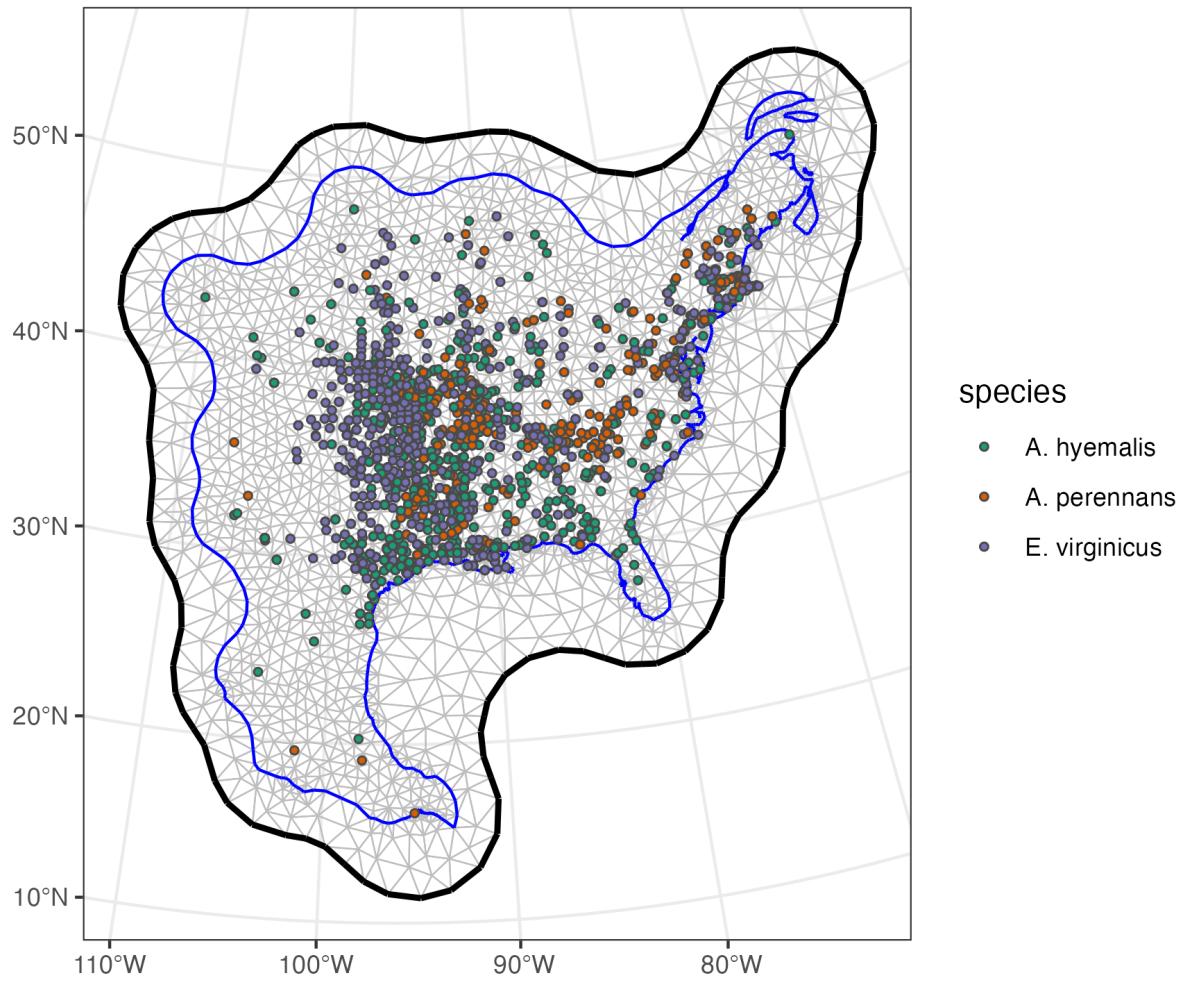


Figure A2: Triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull 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.

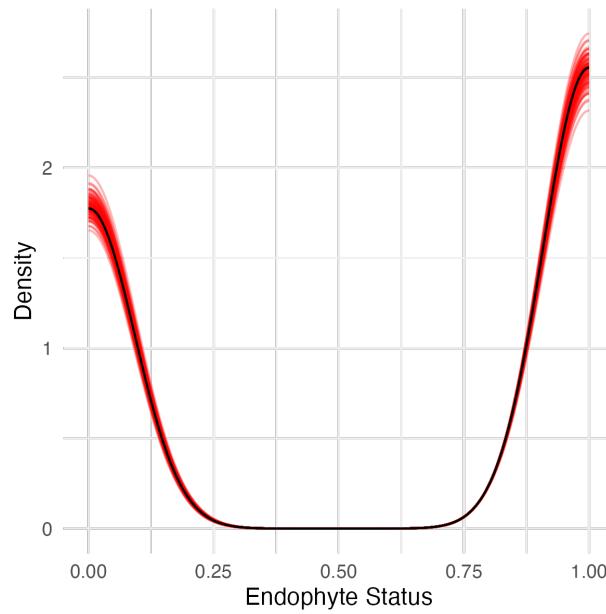


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (black) along with 100 simulated datasets (red).

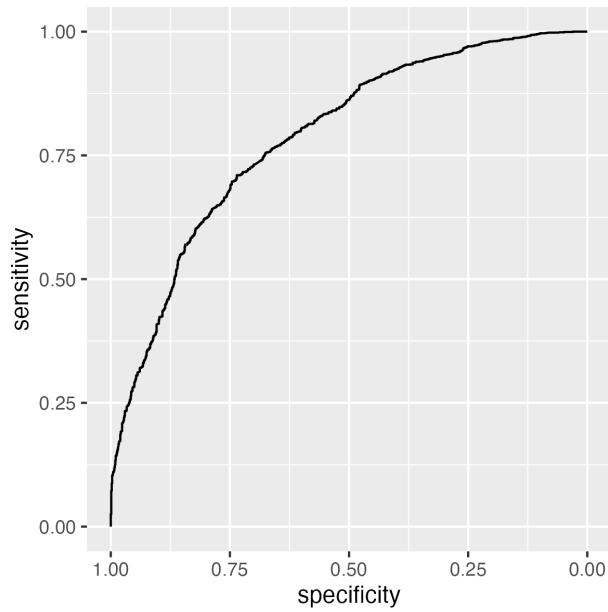


Figure A4: ROC plot showing model performance classifying observations according to endophyte status within the in-sample data. The curves show adequate model performance for observed data. The AUC value is 0.79.

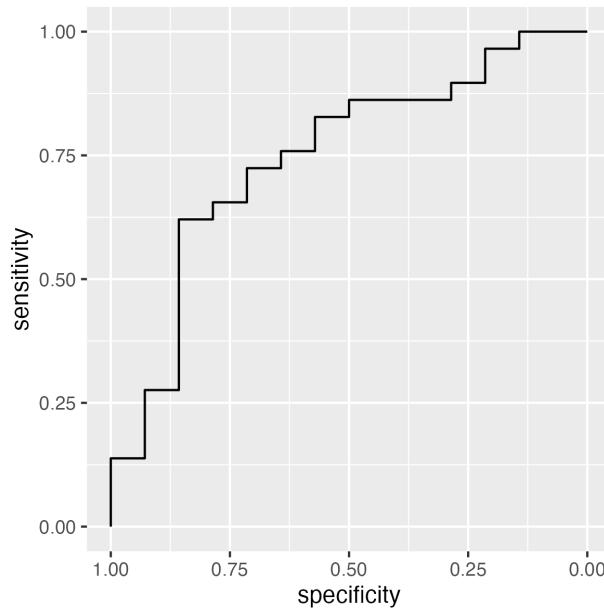


Figure A5: ROC plot showing model performance classifying observations according to endophyte status within the out-of-sample data. The curves show adequate model performance for test data. The AUC value is 0.77.

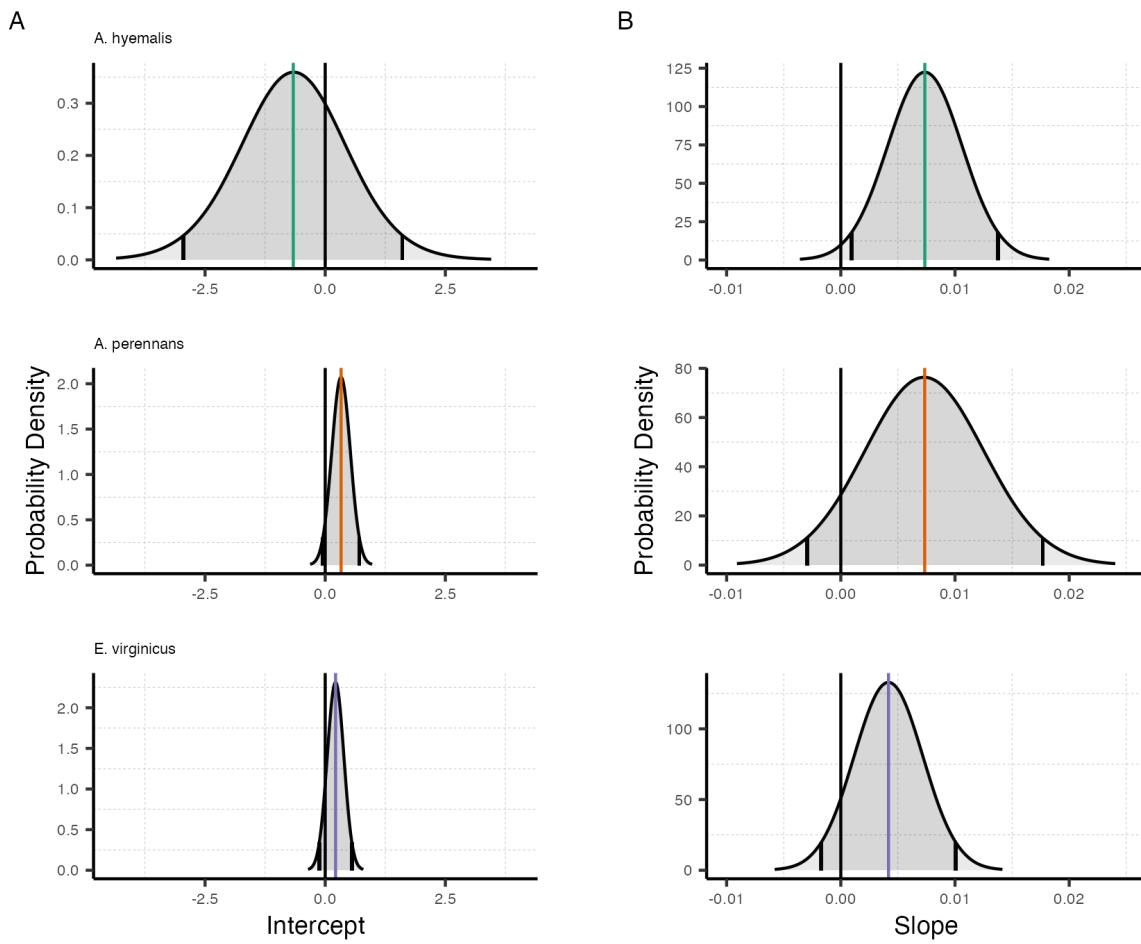


Figure A6: Density curves show the probability density along with mean (colored line) and 95% CI (black lines) for the (A) intercept and (B) slope terms, **A** and **T** respectively. Colors represent each host species

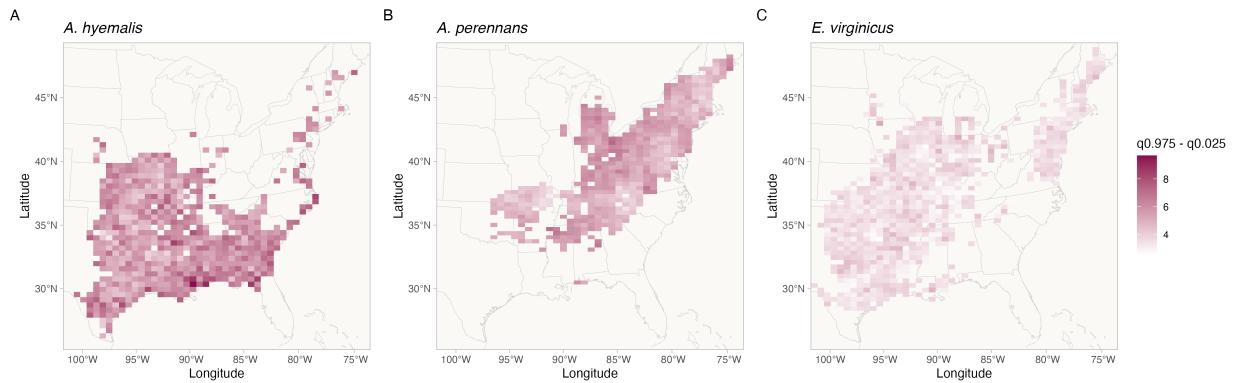


Figure A7: Shading represents the range of the 95% posterior credible interval for spatially varying slopes, τ .

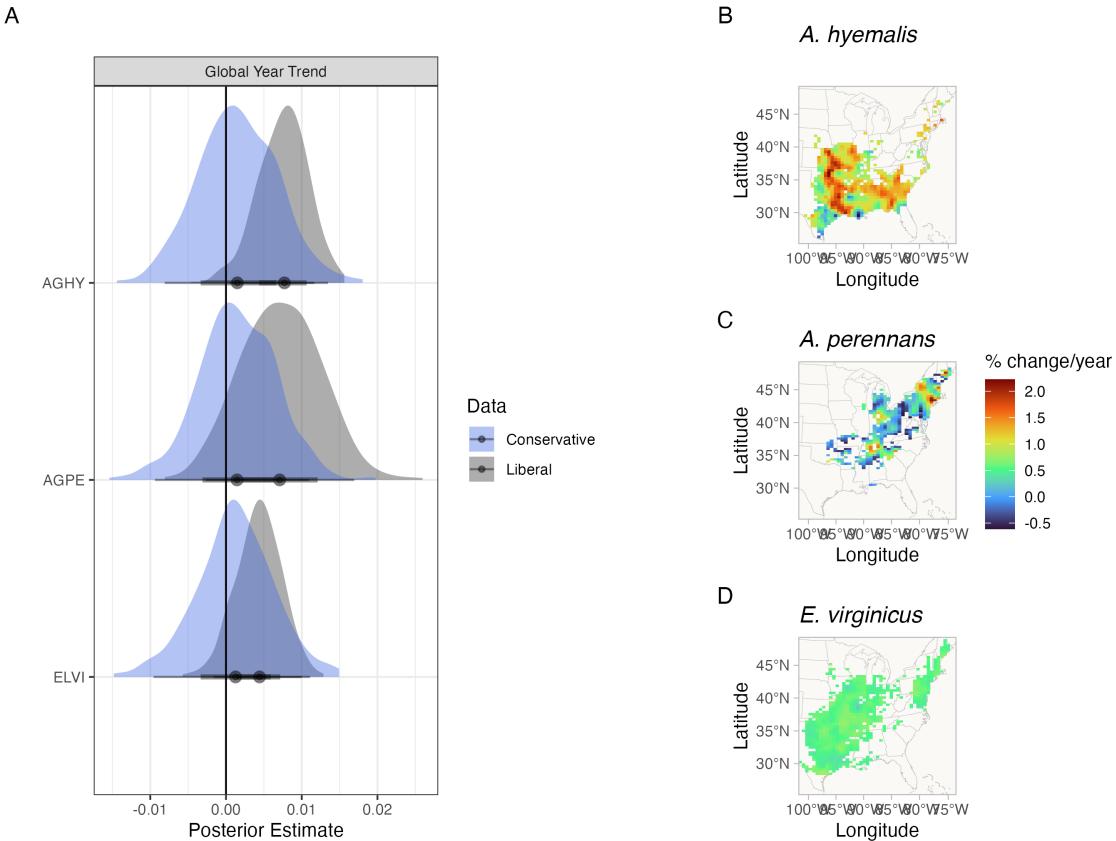


Figure A8: Comparison of liberal versus conservative endophyte scores on modeled outcomes. (A) Posterior estimates of global temporal trend for models fit to liberal scores (grey) and to conservative scores (blue). Maps show the spatially varying temporal trend estimates from model fit to conservative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

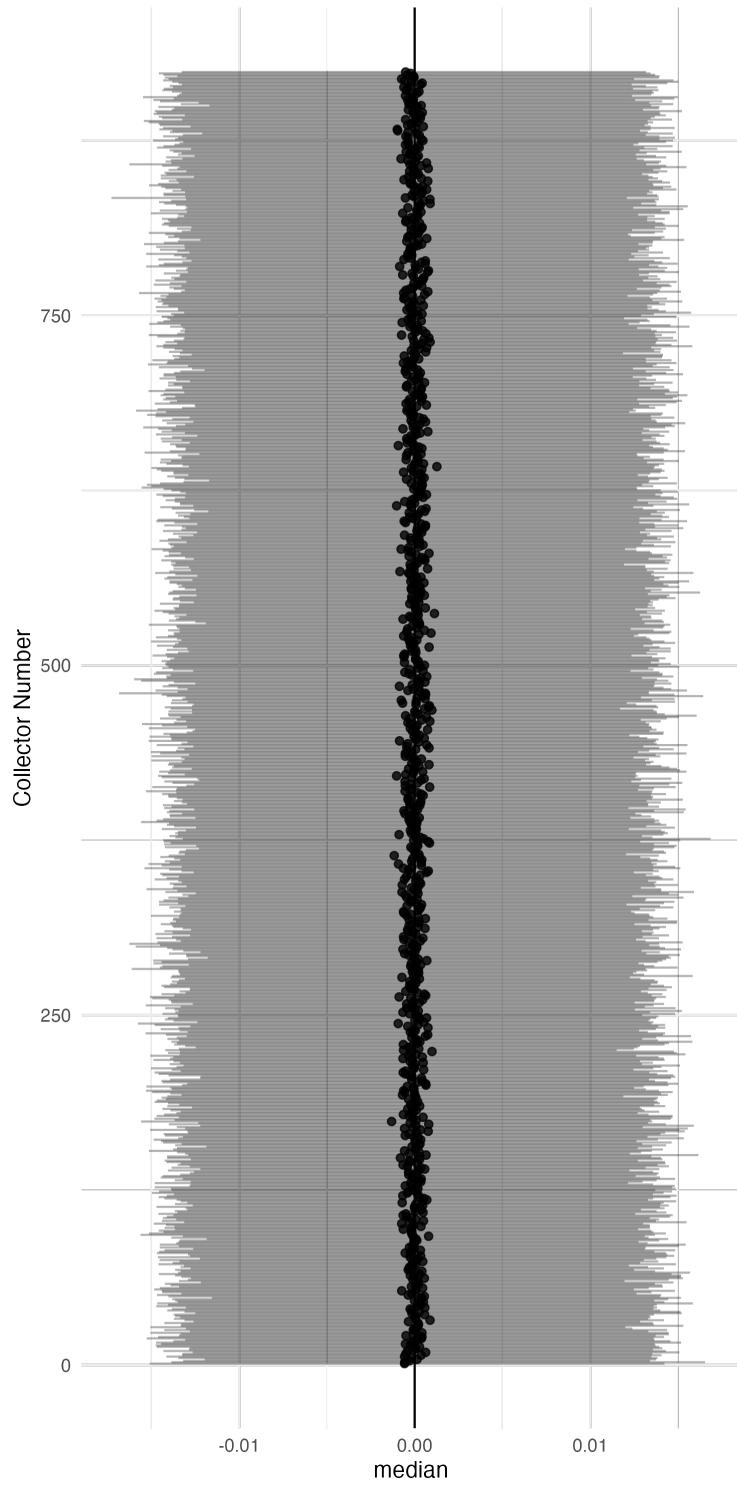


Figure A9: **Posterior estimates of collector random effects.** Points show posterior median along with 95% CI for each of 924 individual collectors.

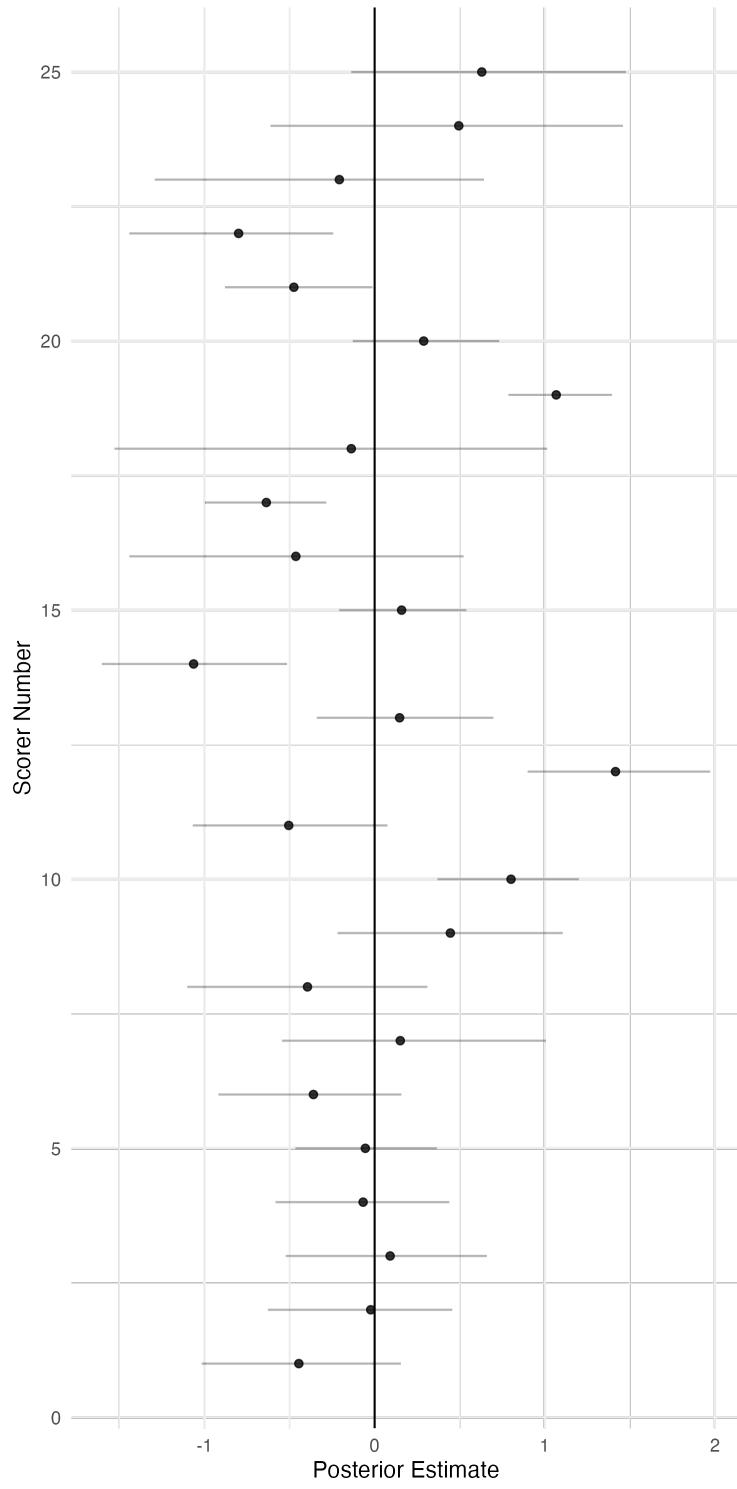


Figure A10: **Posterior estimates of scorer random effects.** Points show posterior median along with 95% CI for each of 25 individual collectors.

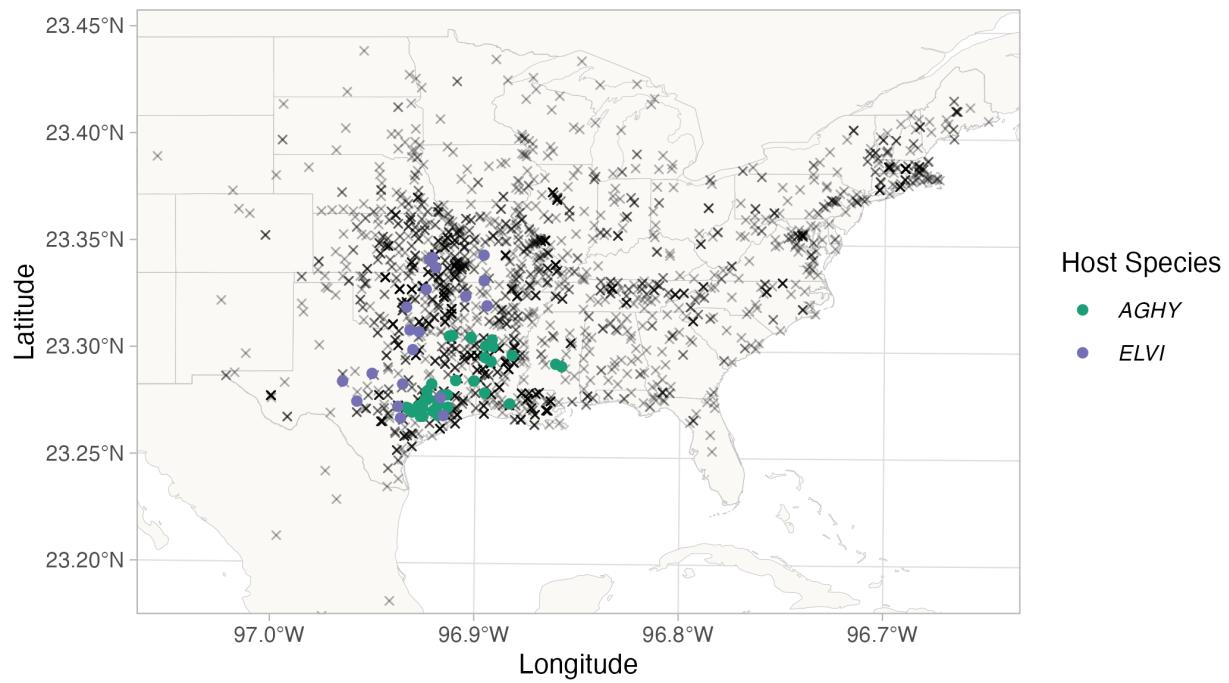


Figure A11: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

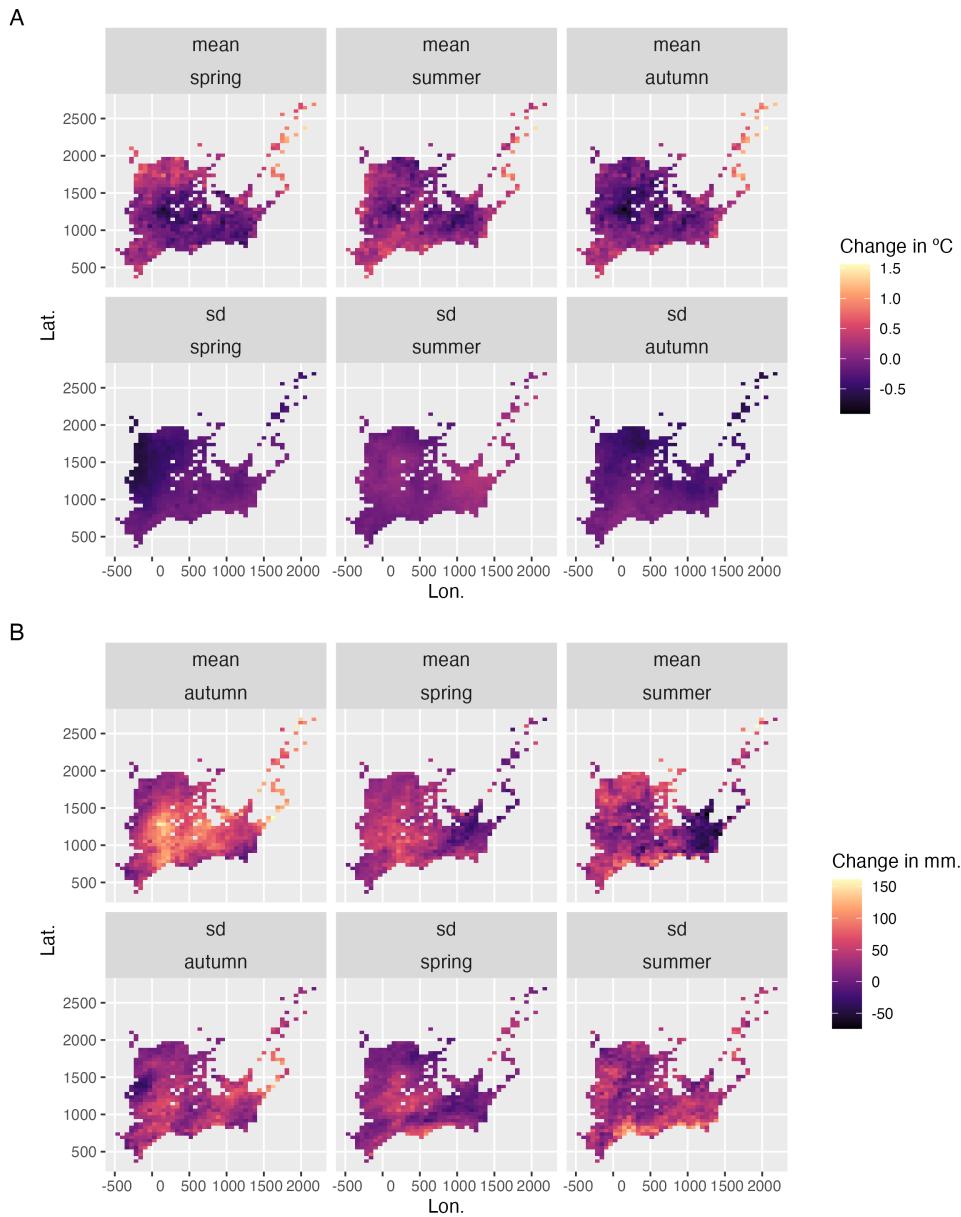


Figure A12: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. hyemalis* used in post-hoc climate correlation analysis.

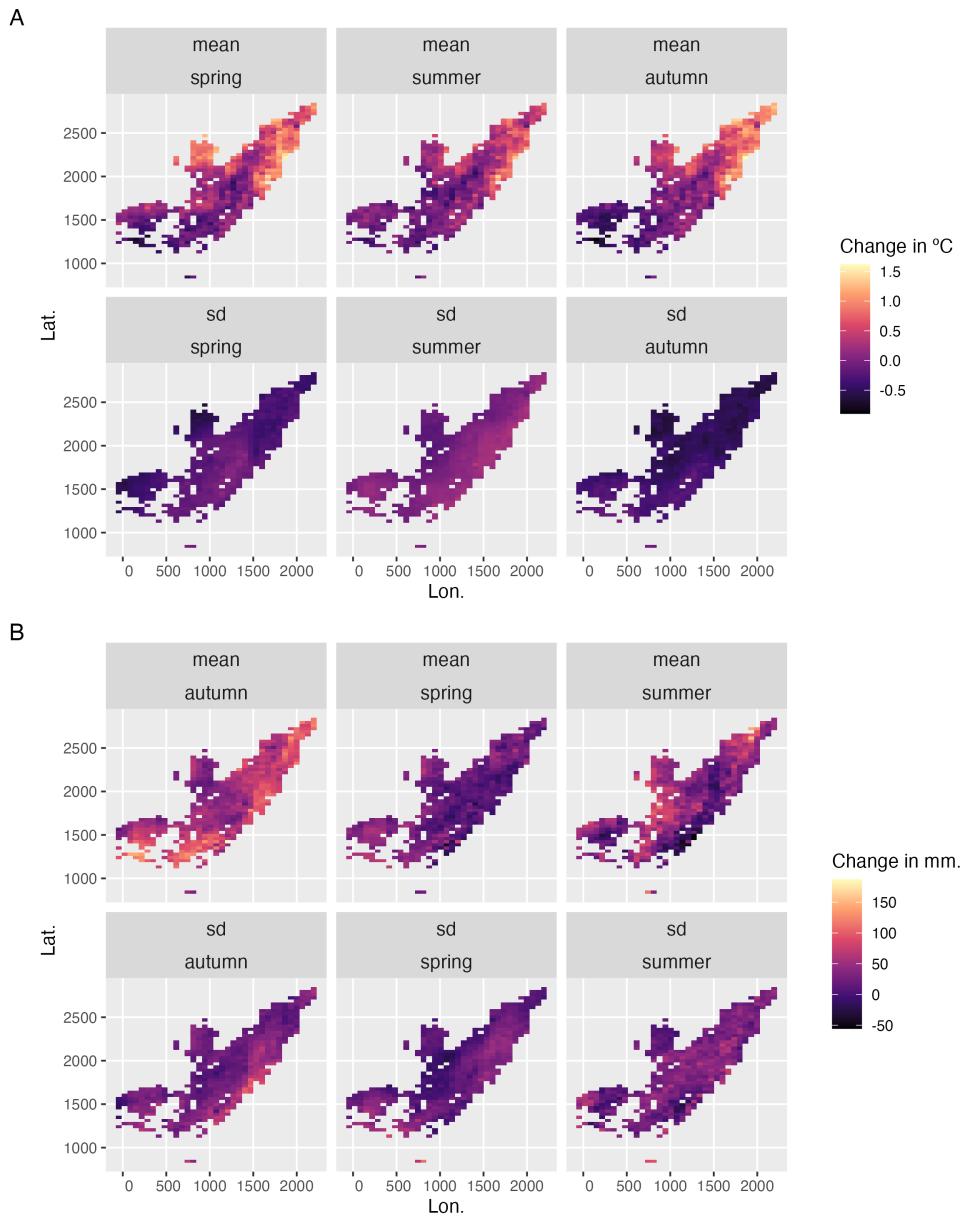


Figure A13: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020.

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.

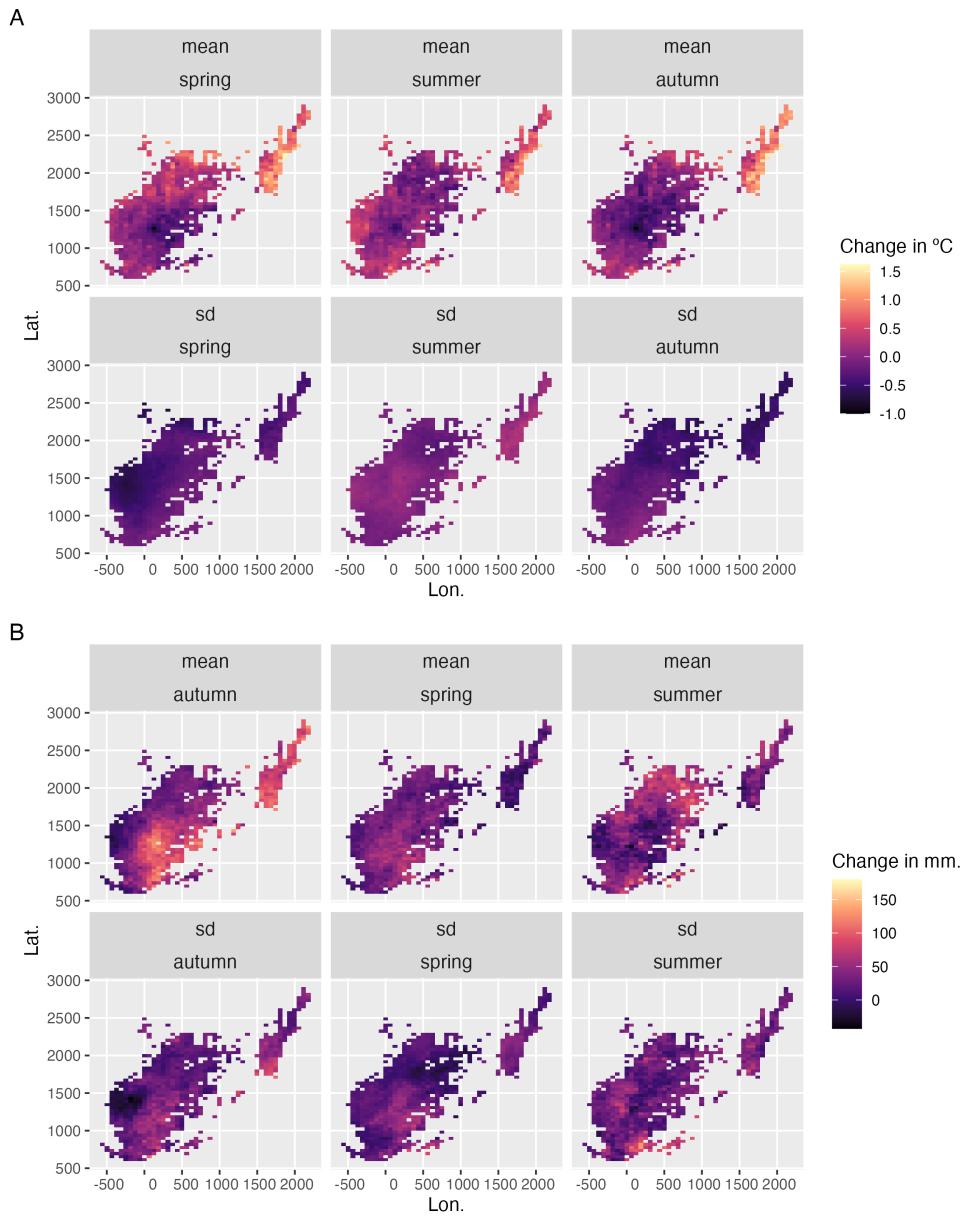


Figure A14: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *E. virginicus* used in post-hoc climate correlation analysis.

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

858

Supporting Methods

859

ODMAP Protocol

860 Overview

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

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

863 **Study area:** Eastern North America

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

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

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

867 **Boundary:** Natural.

868 Data

869 **Observation type:** Occurrence records from Global Biodiversity Information Facility and

870 herbarium collection across eastern North America. We used 713 occurrences records for

871 *Agrostis hyemalis*, 656 occurrence records for *Agrostis perennans* and 2338 for *Elymus virginicus*.

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

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

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

875 **Model**

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

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

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

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

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

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

884 **Assessment**

885 We used AUC to test model performance.

886 **Prediction**

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

889 *Mesh and Prior Sensitivity analysis*

890 To test the influence that the triangulation mesh and choice of priors has on results, we compared
891 model results across a range of meshes and priors. We re-ran our model for the mesh used in
892 main body of the text (Fig. A2), which we refer to as the "standard mesh", and with a mesh with
893 smaller minimum vertices (finer mesh). Finer scale meshes increase computation time. For each
894 of these meshes, we ran the model with a range of priors defining the spatial range of our spatial
895 random effects: 342km (the prior used for presented results), as well as ranges five times smaller
896 (68 km) and five times larger (1714 km). We found generally that these choices did not alter the

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

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

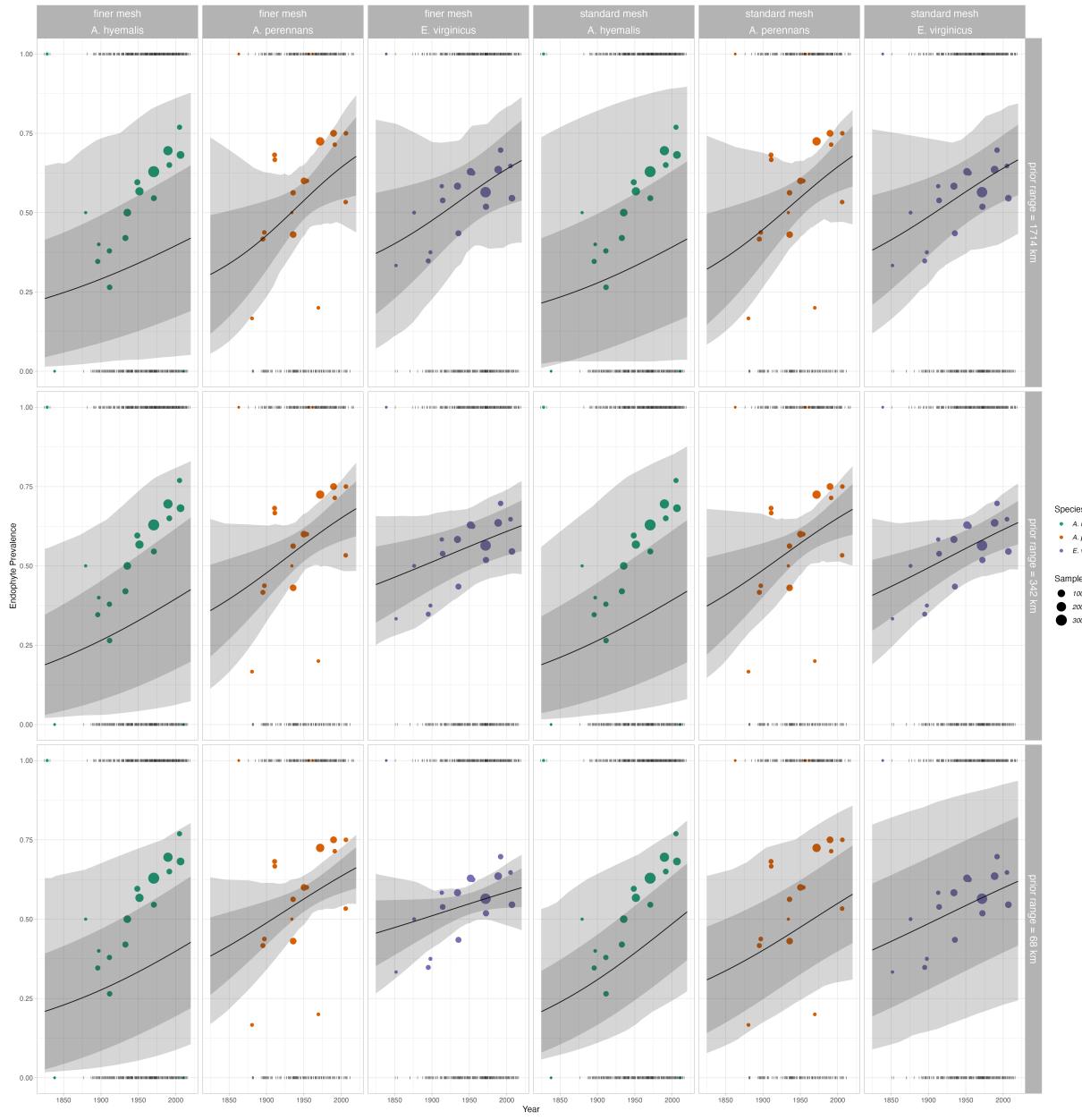


Figure A15: Overall trend in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for two different meshes. Note that these plots, as compared to Fig. 2 in main text, show mean trends and do not incorporate prediction uncertainty associated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

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

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

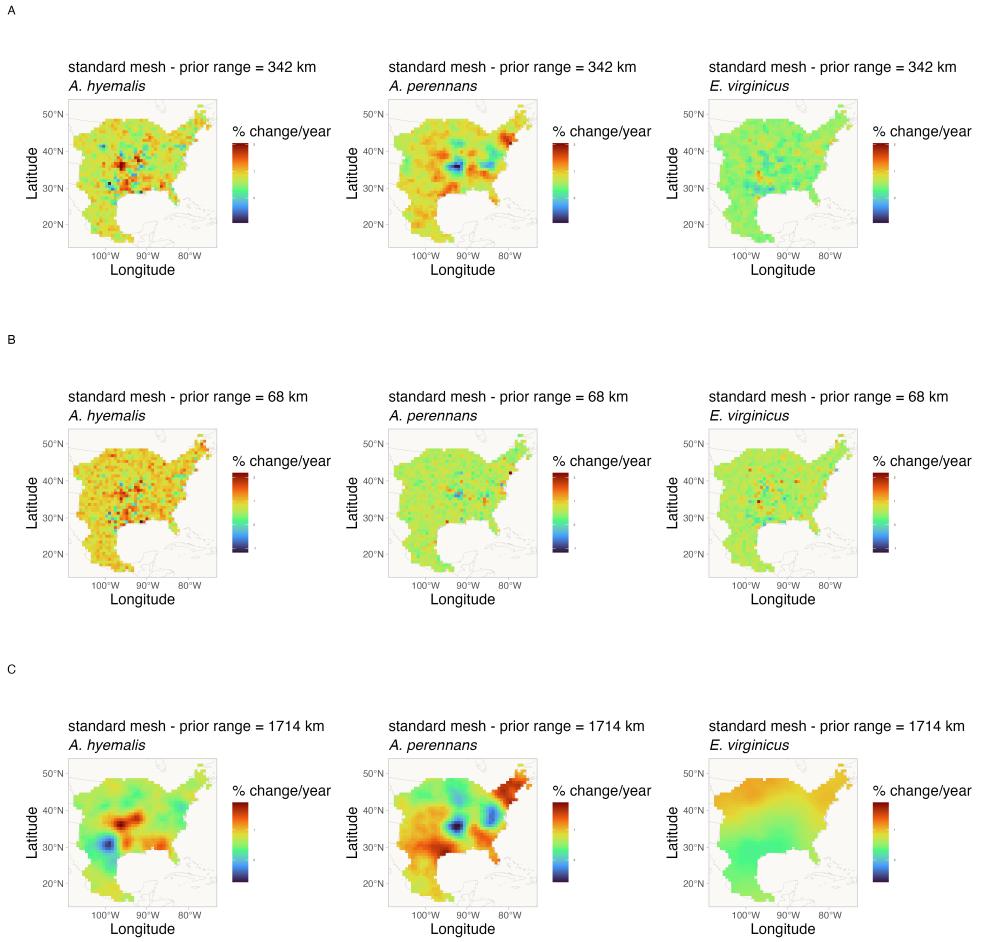


Figure A16: Spatially-varying trends in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for the "standard" mesh. Shading indicates the magnitude and direction of predicted trends for each of three host species for each of three prior ranges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

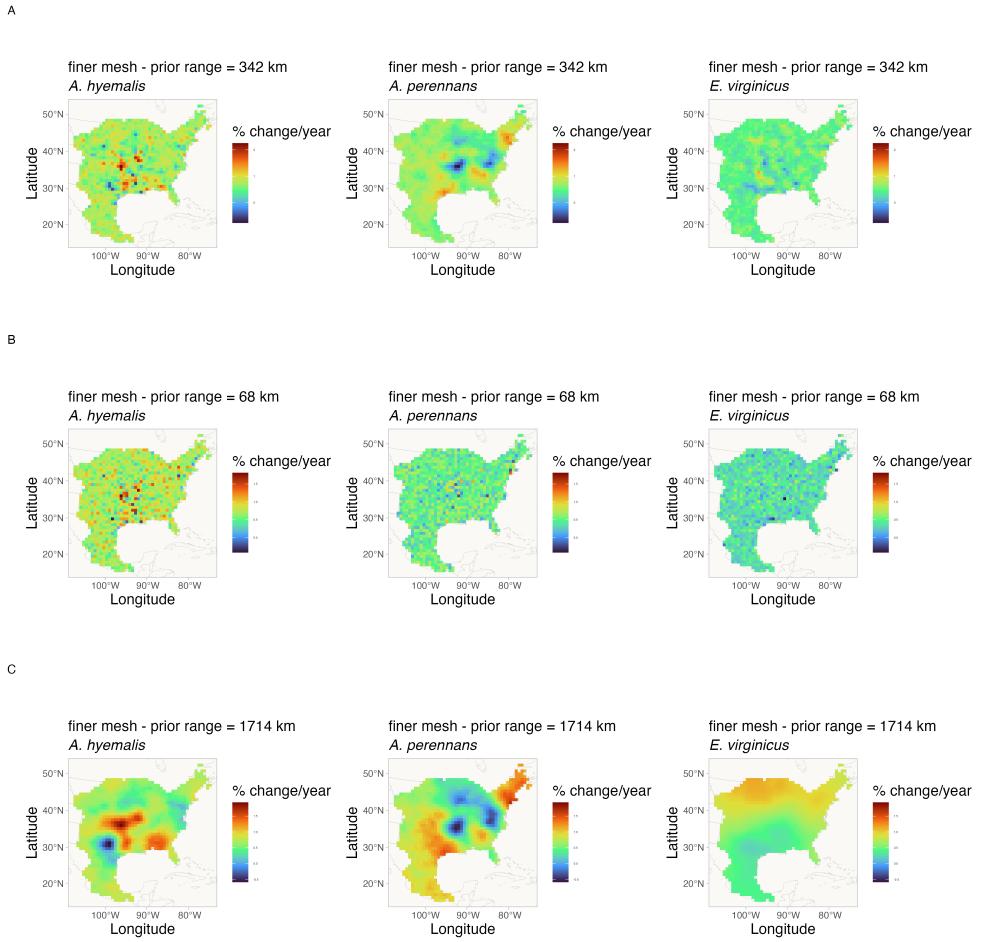


Figure A17: Spatially-varying trends in endophyte prevalence evaluated for models with different range priors on spatially structured random effects, and for the "finer" mesh. Shading indicates the magnitude and direction of predicted trends for each of three host species for each of three prior ranges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