

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

³ Joshua C. Fowler^{1,2*}

Jacob Moutouama¹

Tom E. X. Miller¹

⁴ 1. Rice University, Department of BioSciences, Houston, Texas 77006; 2. University of Miami,
⁵ Department of Biology, Miami, Florida;
⁶ * Corresponding author; e-mail: jcf221@miami.edu.

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Abstract

Species' distributions and abundances are shifting in response to climate change. Most species harbor microbial symbionts that have the potential to influence these responses. Mutualistic microbial symbionts may provide resilience to environmental change by protecting their hosts from increasing stress. However, environmental change that disrupts these interactions may lead to declines in hosts or symbionts. Microbes preserved within herbarium 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 collected over the last two centuries (1824 – 2019) for the presence or absence of endophyte symbiosis, and evaluated spatial and temporal trends in endophyte prevalence. We found that endophytes have increased in prevalence over the last two centuries from ca. 25% prevalence to ca. 75% prevalence, on average, across the three host species. We also found that changes in prevalence were associated with observed changes in seasonal climate drivers¹ corresponding to each host species' peak growing season. Our analysis performed favorably in an out-of-sample predictive test, however we identified XXX as suggesting the model fusion may be an important step moving forward. 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.²

¹Describe "changes" – warming? drying?

²I like this and the abstract in general. I agree with Tom and I think we have some space to add these details. Abstract : 300

Introduction

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

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

55 Microbial symbionts are common to all macroscopic organisms and can have important ef-
56 fects on their hosts' survival, growth and reproduction (McFall-Ngai et al., 2013; Rodriguez et al.,
57 2009). Many microbial symbionts act as mutualists, engaging in reciprocally beneficial interac-
58 tions with their hosts that can ameliorate environmental stress. For example, bacterial symbionts

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

74 Understanding of how microbial symbioses are affected by climate change is additionally
75 complicated by spatial heterogeneity in the direction and magnitude of environmental change
76 (IPCC, 2021). Beneficial symbionts are likely able to shield their hosts from environmental stress
77 in locations that experience a small degree of change, but symbionts in locations that experience
78 changes of large magnitude may be pushed beyond their physiological limits (Webster et al.,
79 2008). Additionally, symbionts are often unevenly distributed across their hosts' distribution.
80 Facultative symbionts may be absent from portions of the host range (Afkhami et al., 2014),
81 and hosts may engage with a diversity of partners (different symbiont species or locally-adapted
82 strains) across their environments (Frade et al., 2008; Rolshausen et al., 2018). Identifying broader
83 spatial trends in symbiont prevalence is therefore an important step in developing predictions
84 for where to expect changes in the symbiosis in future climates.

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

86 documented in ~ 30% of cool-season grass species (Leuchtmann, 1992). They are transmitted ver-
87 tically from maternal plants to offspring through seeds. Vertical transmission creates a feedback
88 between the fitness of host and symbiont (Douglas, 1998; Fine, 1975; Rudgers et al., 2009). Over
89 time, endophytes that act as mutualists should rise in prevalence within a host population (Don-
90 ald et al., 2021). *Epichloë* are known to improve their hosts' drought tolerance (Decunta et al.,
91 2021) and protect their hosts against herbivores (Crawford et al., 2010) and pathogens (Xia et al.,
92 2018) likely through the production of a diverse suite of alkaloids and other secondary metabo-
93 lites. The fitness feedback induced by vertical transmission leads to the prediction that endophyte
94 prevalence should be high in populations where these fitness benefits are most important. Pre-
95 vious contemporary survey studies have documented large-scale spatial patterns in endophyte
96 prevalence structured by environmental gradients (Afkhami, 2012; Bazely et al., 2007; Granath
97 et al., 2007; Sneck et al., 2017). We predicted that prevalence should track temporal changes in
98 environmental drivers that elicit these fitness benefits.

99 Early research on *Epichloë* used herbarium specimens to describe the broad taxonomic di-
100 versity of host species that harbor these symbionts (White and Cole, 1985), establishing that
101 endophyte symbiosis could be identified in plant tissue from as early as 1851.³ However, no
102 subsequent studies, to our knowledge, have used the vast resources of biological collections to
103 quantitatively assess spatio-temporal trends in endophyte prevalence and their environmental
104 correlates. Grasses are commonly collected and identified based on the presence of their re-
105 productive structures, meaning that preserved specimens typically contain seeds, conveniently
106 preserving the fungi along with their host plants on herbarium sheets. This creates the oppor-
107 tunity to leverage the unique spatio-temporal sampling of herbarium collections to examine the
108 response of the symbiosis to historical climate change. Research using historical collections has
109 clearly demonstrated other ecological signatures of a changing climate. However the predictive
110 ability of these historical analyses is rarely tested against contemporary data (Lee et al., 2024).
111 Identifying the ways in which these analyses fall short is a crucial step for the field move from

³Edited this a bit. This is the earliest year we have in the database that was part of JFWhites original paper.

112 reading signatures in the past to forecasting ecological dynamics into the future.⁴

113 In this study, we assessed the long-term responses of endophyte symbiosis to climate change
114 through the use of herbarium specimens of three North American host grass species (*Agrostis*
115 *hyemalis*, *Agrostis perennans*, and *Elymus virginicus*). We first address questions describing spatial
116 and temporal trends in endophyte prevalence: (i) How has endophyte prevalence changed over
117 the past two centuries? and (ii) How spatially variable are temporal trends in endophyte preva-
118 lence across eastern North America? We then address how climate change may be driving trends
119 in endophyte prevalence by asking: (iii) What is the relationship between variation in temporal
120 trends in endophyte prevalence and changes in climate drivers? We predicted that aggregate en-
121 dophyte prevalence would increase over time in tandem with climate warming, and that hotspots
122 of endophyte change would correspond spatially to hotspots of climate change. Finally, we eval-
123 uated the performance of models built on data from historic specimens with an out-of-sample
124 test, data on endophyte prevalence from contemporary surveys of host populations. To answer
125 these questions we examined a total of 2,346 specimens collected across eastern North America
126 between 1824 and 2019.⁵

127 Methods

128 Focal species

129 Our surveys focused on three native North American grasses: *Agrostis hyemalis*, *Agrostis peren-*
130 *nans*, and *Elymus virginicus*. Both *Agrostis* species host *Epichloë amarillans* (Craven et al., 2001;
131 Leuchtmann et al., 2014), while *Elymus virginicus* typically hosts *Epichloë elymi* (Clay and Schardl,
132 2002). These C₃ grass species are commonly represented in natural history collections with broad
133 distributions covering much the eastern United States. *A. hyemalis* is a small short-lived perennial

⁴*what do you think of this? trying to presage the out-of-sample test without over promising and without saying outright that our analysis sucks. Is this the right place for this? I had imagined some of this material will be really developed in the discussion.*

⁵*I think the consensus was to keep the out-of-sample validation which should absolutely go into the Intro as an important element of novelty. Should go in the Abstract too.*

¹³⁴ species that germinates in the spring and typically flowers between March and July (most com-
¹³⁵ mon collection month: May). *A. perennans* is of similar stature but is longer lived than *Agrostis*
¹³⁶ *hyemalis* and flowers in late summer and early autumn (most common collection month: Septem-
¹³⁷ ber). *A. perennans* is more sparsely distributed, tending to be found in shadier and more moist
¹³⁸ habitats, while *A. hyemalis* is commonly found in open and recently disturbed ground. Both
¹³⁹ *Agrostis* species are recorded from throughout the Eastern US, but *A. perennans* has a slightly
¹⁴⁰ more northern distribution, whereas *A. hyemalis* is found rarely as far north as Canada and is
¹⁴¹ listed as a rare plant in Minnesota. *E. virginicus* is a larger and relatively longer-lived species that
¹⁴² is more broadly distributed than the *Agrostis* species. It begins flowering as early as March or
¹⁴³ April but continues throughout the summer (most common collection month: July).

¹⁴⁴ *Herbarium surveys*

¹⁴⁵ We visited nine herbaria between 2019 and 2022 (see Table A1 for a summary of specimens in-
¹⁴⁶ cluded from each collection). With permission from herbarium staff, we acquired seed samples
¹⁴⁷ from 1135 *A. hyemalis* specimens collected between 1824 and 2019, 357 *A. perennans* specimens
¹⁴⁸ collected between 1863 and 2017, and 854 *E. virginicus* specimens collected between 1839 and
¹⁴⁹ 2019 (Fig. 1, Fig. 2A, Fig. A1). We chose our focal species in part because they are commonly
¹⁵⁰ represented in herbarium collections, and produce high numbers of seeds, meaning that small
¹⁵¹ samples would not diminish the value of the specimens for future studies. We collected 5-10
¹⁵² seeds per specimen after examining the herbarium sheet under a dissecting microscope to en-
¹⁵³ sure that we collected mature seeds, not florets or unfilled seeds, fit for our purpose of identifying
¹⁵⁴ fungal endophytes with microscopy. We excluded specimens for which information about the
¹⁵⁵ collection location and date were unavailable. Each specimen was assigned geographic coor-
¹⁵⁶ dinates based on collection information recorded on the herbarium sheet using the geocoding
¹⁵⁷ functionality of the ggmap R package (Kahle et al., 2019). Many specimens had digitized collec-
¹⁵⁸ tion information readily available, but for those that did not, we transcribed information printed
¹⁵⁹ on the herbarium sheet. Collections were geo-referenced to the nearest county centroid, or near-

¹⁶⁰ est municipality when that information was available. For a few of the oldest specimens, only
¹⁶¹ information at the state level was available, and so we used the state centroid.

¹⁶² After collecting seed samples, we quantified the presence or absence of *Epichloë* fungal hy-
¹⁶³ phae, which grow intercellularly, in each specimen using microscopy. We first softened seeds
¹⁶⁴ with a 10% NaOH solution, then stained the seeds with aniline blue-lactic acid stain and squashed
¹⁶⁵ them under a microscope cover slip. We examined the squashed seeds for the presence of fungal
¹⁶⁶ hyphae at 200-400X magnification (Bacon and White, 2018). In some cases, the tissues examined
¹⁶⁷ during microscopy came from flowers or otherwise non-viable seeds, which were excluded for
¹⁶⁸ that specimen. On average we scored 4.7 seeds per specimen of *A. hyemalis*, 4.2 seeds per spec-
¹⁶⁹ imen of *A. perennans*, and 3.8 seeds per specimen of *E. virginicus*; we scored # seeds in total. .
¹⁷⁰ Due to imperfect vertical transmission (Afkhami and Rudgers, 2008), it is possible that symbiotic
¹⁷¹ host-plants produce a mixture of symbiotic and non-symbiotic seeds. We therefore designated a
¹⁷² specimen as endophyte-symbiotic if *Epichloë* hyphae were observed in one or more of its seeds,
¹⁷³ or non-symbiotic if hyphae were observed in none of its seeds. To capture uncertainty in the
¹⁷⁴ endophyte scoring process, we recorded both a "liberal" and a "conservative" endophyte status
¹⁷⁵ for each plant specimen. When we identified potential endophytes with unusual morphology,
¹⁷⁶ low uptake of stain, or a small amount of fungal hyphae across the scored seeds, we recorded a
¹⁷⁷ positive liberal status (more likely to be endophyte-positive) and a negative conservative status
¹⁷⁸ (less likely to be endophyte-positive). 89% of scored plants had matching liberal and conservative
¹⁷⁹ scores, reflecting high confidence in endophyte status. The following analyses in the main text
¹⁸⁰ used the liberal status, but we repeated all analyses with the conservative status which yielded
¹⁸¹ qualitatively similar results (Fig. ??)

¹⁸² *Modeling spatial and temporal changes in endophyte prevalence*

¹⁸³ We assessed spatial and temporal changes in endophyte prevalence across each host distribution,
¹⁸⁴ quantifying the "global" temporal trends, aggregating across space, and then examining spatial
¹⁸⁵ heterogeneity in the direction and magnitude of endophyte change (hotspots and coldspots)

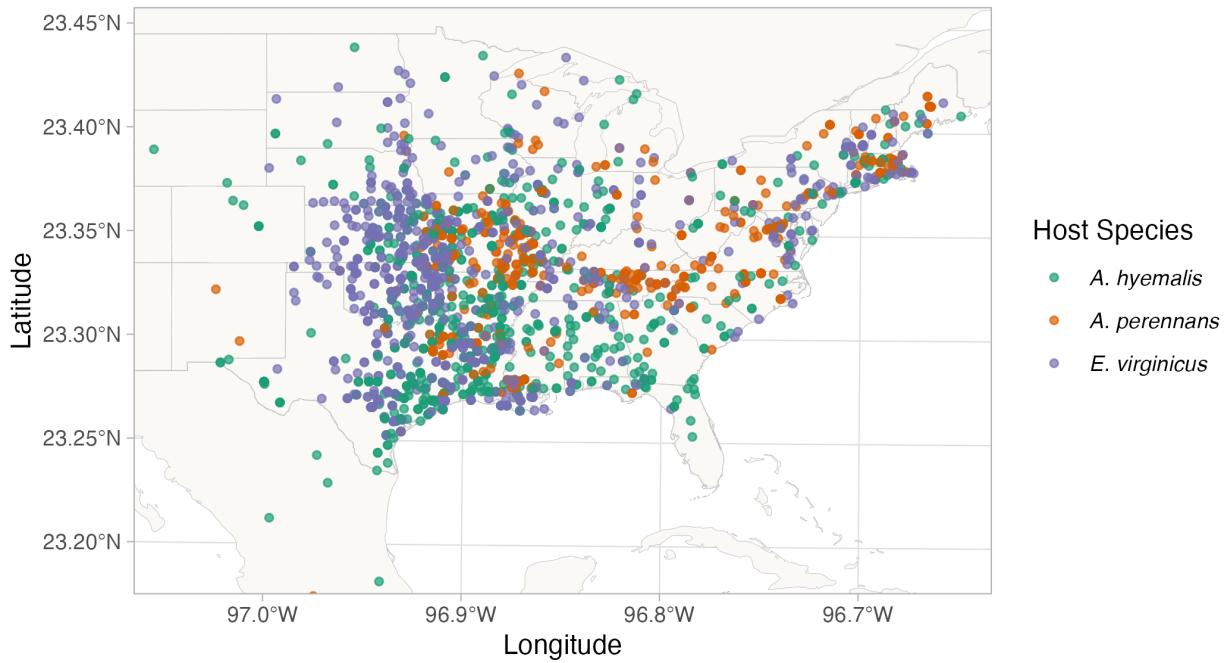


Figure 1: Collection locations of herbarium specimens of three grass host species across eastern North America that were sampled for *Epichloë* endophyte presence or absence.

across the spatial extent of each host's distribution. To appropriately account for the spatial non-independence of geo-referenced occurrences⁶, we used an approximate Bayesian method, Integrated Nested Laplace Approximation (INLA), to construct spatio-temporal models of endophyte prevalence. INLA provides a computationally efficient method of ascertaining parameter posterior distributions for certain models that can be formulated as latent Gaussian Models (Rue et al., 2009). Many common statistical models, including structured and unstructured mixed-effects models, can be represented as latent Gaussian Models. We incorporated spatial heterogeneity into this analysis using spatially-structured intercept and slope parameters implemented as stochastic partial differential equation (SPDE) approximations of a continuous spatial Gaussian process. This SPDE approach is a flexible method of smoothing across space while explicitly accounting for spatial dependence between data-points (Bakka et al., 2018; Lindgren et al., 2011).

⁶spelling?

197 Fitting models with structured spatial effects is possible with MCMC sampling but can require
 198 long computation times, making INLA an effective alternative, which has been used to model
 199 spatial patterns in flowering phenology (Willems et al., 2022), the abundance of bird species
 200 (Meehan et al., 2019) and butterflies (Crossley et al., 2022), the distribution of temperate trees
 201 (Engel et al., 2022) as well as the population dynamics of endangered amphibians (Knapp et al.,
 202 2016) and other ecological processes (Beguin et al., 2012).

203 We estimated global and spatially-varying trends in endophyte prevalence using a joint-
 204 likelihood model. For each host species h , endophyte presence/absence of the i^{th} specimen ($P_{[h]i}$)
 205 was modeled as a Bernoulli response variable with expected probability of endophyte occurrence
 206 $\hat{P}_{[h]i}$. We modeled $\hat{P}_{[h]i}$ as a linear function of intercept $A_{[h]i}$ and slope $T_{[h]}$ defining the global trend
 207 in endophyte prevalence specific to each host species as well as with spatially-varying intercepts
 208 $\alpha_{[h_1]l[i]}$ and slopes $\tau_{[h_1]l[i]}$ associated with location ($l[i]$, a unique latitude-longitude combination).
 209 The joint-model structure allowed us to share variance terms across focal species to account for
 210 dependence associated with the collection of specimens and identification of endophytes. Shared
 211 variance terms included the spatially-dependent random effect $\delta_{l[i]}$, intended to account for resid-
 212 ual spatial variation, and $\chi_{c[i]}$ and $\omega_{s[i]}$ i.i.d.-random effects indexed for each collector identity
 213 ($c[i]$), and scorer identity ($s[i]$) of the i^{th} specimen.

$$\text{logit}(\hat{P}_{[h_1]i}) = A_{[h_1]i} + T_{[h_1]} * \text{year}_i + \alpha_{[h_1]l[i]} + \tau_{[h_1]l[i]} * \text{year}_i + \delta_{l[i]} + \chi_{c[i]} + \omega_{s[i]} \quad (1a)$$

$$\text{logit}(\hat{P}_{[h_2]i}) = A_{[h_2]i} + T_{[h_2]} * \text{year}_i + \alpha_{[h_2]l[i]} + \tau_{[h_2]l[i]} * \text{year}_i + \delta_{l[i]} + \chi_{c[i]} + \omega_{s[i]} \quad (1b)$$

$$\text{logit}(\hat{P}_{[h_3]i}) = A_{[h_3]i} + T_{[h_3]} * \text{year}_i + \alpha_{[h_3]l[i]} + \tau_{[h_3]l[i]} * \text{year}_i + \delta_{l[i]} + \chi_{c[i]} + \omega_{s[i]} \quad (1c)$$

214 Previous work suggests that behavior of historical botanists and uneven sampling may intro-
 215 duce biases into ecological inferences made from historic collections (Kozlov et al., 2020). Prolific
 216 collectors who contribute thousands of specimens may be more or less likely to collect certain
 217 species, or specimens with certain traits (Daru et al., 2018). Similarly, the process of scoring seeds
 218 for hyphae involved several student researchers who, even with standardized training, may vary
 219 in their likelihood of positively identifying *Epichloë* hyphae. By including a random effect for

220 collectors and for scorers, we attempted to account for variance across individual researchers
221 that may bias our predictions of changes in endophyte prevalence.

222 We performed model fitting using the `inlabru` R package ()⁷. Global intercept and slope
223 parameters A, and T, were given vague priors. Scorer and collector random effects, χ and ω ,
224 were given penalized complexity priors, with distributions approximating a Normal distribution
225 with standard deviation of 5. Each spatially-structured parameter depended on a covariance
226 matrix according to the proximity of each collection location (Bakka et al., 2018; Lindgren et al.,
227 2011). The covariance matrix was approximated using a Matérn covariance function, with each
228 data point assigned a location according to the nodes of a mesh of non-overlapping triangles
229 encompassing the study area (Fig. A2). Priors, termed "range" and "variance", define the distance
230 of spatial decay described by the Matérn covariance function. Priors for results presented in the
231 main text reflect a range of XX⁸ kilometers. We found that model results were sensitive to
232 this choice, and so tested a range of priors (from XX kilometers to XX kilometers) and meshes
233 (Supplemental Material), finding that model results were qualitatively similar, i.e. the same
234 direction of effects across space, but that the magnitude and uncertainty varied.

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

236 We evaluated the predictive ability of the model using both in-sample training data from the
237 herbarium surveys, and with out-of-sample test data from contemporary endophyte surveys, **an**
238 **important but rarely used strategy in ecological studies (Tredennick et al., 2021)**.^{9 10} We used
239 data from contemporary surveys of endophyte prevalence in *A. hyemalis* and *E. virginicus* in Texas
240 and the southern US. Surveys of *E. virginicus* were conducted in 2013 as described in Sneed et al.

⁷*add citation*

⁸

⁹*This is the type of thing to emphasize in the intro? Are there any other collections-based papers that have done anything like this?? None to my knowledge.*

¹⁰*Add Benjamin lee paper, maybe? it's not just herbaria, but kind of related*

241 (2017), and surveys of *A. hyemalis* took place between 2015 and 2020¹¹. Population surveys of *A.*
242 *hyemalis* were initially designed to cover longitudinal variation in endophyte prevalence towards
243 its range edge, while surveys of *E. virginicus* were designed to cover latitudinal variation along its
244 range edge. In total, we visited 43 populations of *A. hyemalis* and 20 populations of *E. virginicus*
245 across the south-central US, with emphasis on Texas and neighboring states (Fig A11). During
246 surveys, we collected seeds from up to 30 individuals per location (average number of plants
247 sampled: 22.9). We quantified the endophyte status of each individual with staining microscopy
248 as described for the herbarium surveys (with 5-10 seeds scored per individual), and calculated
249 the prevalence of endophytes within the population (proportion of symbiotic plants divided by
250 the number of sampled plants). For each population, we compared the observed fraction of
251 endophyte-symbiotic hosts to the predicted probability of endophyte occurrence \hat{P} derived from
252 the model based on location and year. The contemporary survey period (2013-2020) is at the most
253 recent edge of the time period encompassed by the historical observations used for model fitting.
254 We compared the model's prediction for these locations to the observed population prevalence.

255 *Assessing the role of climate drivers*

256 We assessed how the magnitude of climate change may have driven changes in endophyte preva-
257 lence by assessing correlations between changes in climate and changes in endophyte prevalence
258 predicted from our spatial model at evenly spaced pixels across the study area. We first down-
259 loaded monthly temperature and precipitation rasters from the PRISM climate group (Daly and
260 Bryant, 2013) covering the time period between 1895 and 2020 using the 'prism' R package (Hart
261 and Bell, 2015). Prism provides reconstructions of historic climate variables across the United
262 States by spatially-interpolating weather station data (Di Luzio et al., 2008). We calculated 30-
263 year climate normals for seasonal mean temperature and cumulative precipitation for the recent
264 (1990 to 2020) and historic (1895 to 1925) periods. We used three four-month seasons within

¹¹We have added more recent AGHY survey data. I am not sure if you have access to this but you should definitely use it. Karl or I can point you to the right file.

265 the year (Spring: January, February, March, April; Summer: May, June, July, August; Autumn:
266 September, October, November, December). This division of seasons allowed us to quantify dif-
267 ferences in climate associated with the two “cool” seasons, when we expected our focal species
268 to be most biologically active (*A. hyemalis* flowering phenology: spring; *E. virginicus*: spring and
269 summer; *A. perennans*: autumn). In addition to mean climate conditions, environmental vari-
270 ability itself can influence population dynamics (Tuljapurkar, 1982) and changes in variability
271 are a key prediction of climate change models (IPCC, 2021; Stocker et al., 2013). Therefore, we
272 calculated the standard deviation for each annual and seasonal climate driver across each 30-
273 year period. We then took the difference between recent and historic periods for the mean and
274 standard deviation for each climate driver (Figs. A12-A14). All together, we assessed twelve
275 potential climate drivers: the mean and standardization of spring, summer, and autumn temper-
276 ature, as well as the mean and standard deviation of spring, summer, and autumn cumulative
277 precipitation, cumulative precipitation, and cumulative precipitation.

278 To evaluate whether areas that have experienced the greatest changes in endophyte preva-
279 lence (hotspots of endophyte change) are associated with high degrees of change in climate
280 (hotspots of climate change), we modeled spatially varying slopes of endophyte change through
281 time ($\tau_{[h]l}$ as a linear function of environmental covariates, with a Gaussian error distribution.¹²
282 Data from each host species was analyzed separately. Fitting regressions to many pixels across
283 the study region risks artificially inflating confidence in our results due to large sample sizes,
284 and so we performed this analysis using only a random subsample of 250 pixels across the study
285 region, which provided results qualitatively similar to analysis of the full set of pixels^{13,14}.

286 15

¹²I think we need to account for uncertainty in the slopes. They are outputs of a (quasi) Bayesian model so we should be able to propagate all the uncertainty in the posterior distribution.

¹³100 seems like a low number to me. What if we did this for all of the herbarium collection locations?

¹⁴I upped the number of points. I don't think conceptually we need to only do collection locations, but I can work on that as an alternative.

¹⁵I cut the notation for the Gaussian model for now because it is a pretty simple model and the notation may be overkill, plus because I changed your tau's to beta's there were betas on both sides of the tilde, which was confusing/annoying. Happy have the

287

Modeling distributions of host species

288 We modeled the distribution of each host species to generate maps on which we predicted the
289 dynamics of *Epichloë* symbionts. We followed the ODMAP (overview, data, model, assessment,
290 prediction) protocol (Crossley et al., 2022). A full description of the ODMAP can be found in the
291 (Supplementary Method ??). Here we presented the workflow of the species distribution model.
292 We used presence-only observations of the host species from Global Biodiversity Information Fa-
293 cility (GBIF) between 1990 to 2020. To reduce the potential influence of sampling bias and spatial
294 autocorrelation, we thinned the occurrences to the spatial scale of our selected climatic predictors.
295 We selected climate variables that aligned with our analysis of climatic influences on trends in
296 endophyte prevalence described above. These climatic variables are: the mean and standard de-
297 viation of spring, summer, and autumn temperature, as well as the mean and standard deviation
298 of spring, summer, and autumn cumulative precipitation, cumulative precipitation, and cumula-
299 tive precipitation. Among this suite of variables, we chose to include mean summer temperature,
300 standard deviation of spring temperature, standard deviation of summer temperature, standard
301 deviation of spring precipitation, standard deviation of summer precipitation, which were uncor-
302 related (Variance Inflation Factor > 0.7) and allowed us to predict the occurrence probability of
303 each host species in space and time. We fit maximum entropy (MaxEnt) models using the max-
304 ent function in the package dismo (Hijmans et al., 2017). We generated 10,000 pseudo-absences
305 as background points, and split the occurrence data into 75% for model training and 25% for
306 model testing. The performance of models was evaluated with AUC (Jiménez-Valverde, 2012).
307 We found AUC = 0.862, AUC = 0.838, AUC = 0.821 respectively for *Agrostis hyemalis*, *Agrostis*
308 *perennans*, and *Elymus virginicus*.

309 To convert the continuous predicted probabilities into binary presence - absence maps, we
310 used the training sensitivity (true positive rate) and specificity threshold (true negative rate) (Liu
notation back if you prefer it. I am also a little confused because the appendix has spearman correlations but there are no methods here for where those come from.

³¹¹ et al., 2005). These binary maps serve as boundaries in presented maps of change in endophyte
³¹² prevalence, and outline the set of pixels used in our analysis of climate correlates with trends in
³¹³ endophyte prevalence.

³¹⁴ **Results**

³¹⁵ *How has endophyte prevalence changed over time?*

³¹⁶ We found that endophyte prevalence increased within the examined specimens over the last two
³¹⁷ centuries for all three host species (Fig. 2). On average, modeling indicated that endophytes of *A.*
³¹⁸ *perennans* and *E. virginicus* increased from ~ 40 % to 70% prevalence across the study region, and
³¹⁹ that of *A. hyemalis* increased from ~ 25% to over 50% prevalence. Our model indicates a high
³²⁰ certainty that overall temporal trends are positive across species (99% probability of a positive
³²¹ overall year slope in *A. hyemalis*, 92% probability of a positive overall year slope in *A. perennans*,
³²² and 91% probability of a positive overall year slope in *E. virginicus*) (Fig. A6)

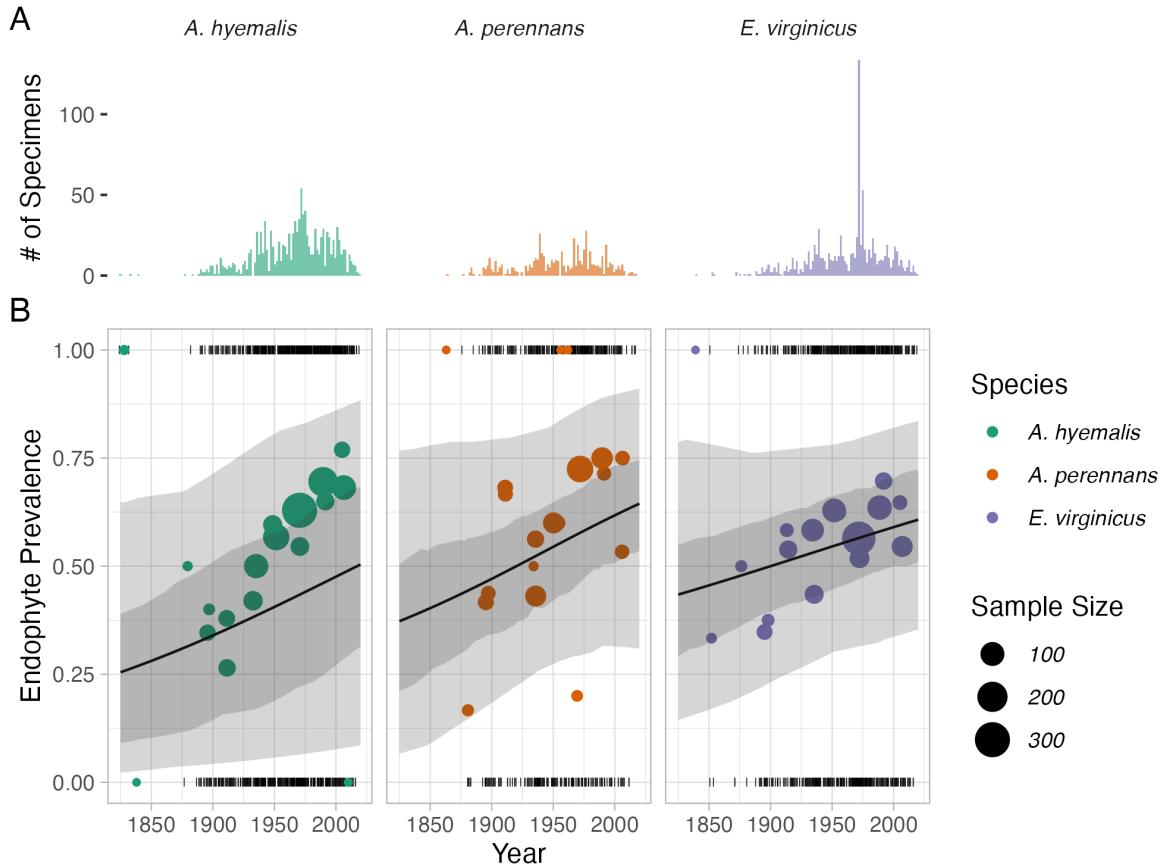


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of scored specimens through time for each host species. (B) Lines show predicted mean endophyte prevalence over the study period along with the 50% and 95% CI bands incorporating uncertainty associated with collector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

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

324 Our model revealed hotspots of change in endophyte prevalence. While there was an overall
 325 increase in endophyte prevalence, these changes varied across the host species' ranges (Fig. 3).
 326 In some regions, posterior estimates of spatially varying temporal trends, τ , indicate that *A.*

327 *hyemalis* and *A. perennans* experienced increases in percent prevalence by as much as 2% per
 328 year over the study period, while *E. virginicus* experienced increases up to around 1% per year.
 329 Compared to *E. virginicus*, which had a weaker overall increase in endophytes and less spatial
 330 variability, maps of both *Agrostis* species show areas of strong increase and areas of declining
 331 prevalence. Notably, endophytes increased towards the western range edge of *A. hyemalis* (Fig.
 332 3A) and across the northeastern US for *A. perennans* (Fig. 3B). Posterior estimates of uncertainty
 333 in spatially varying slopes indicate that these hotspots of change may have experienced increases
 334 of up to 5% per year while declines in prevalence may be as great as 4% per year for *A. hyemalis*
 335 and *A. perennans*. For *E. virginicus*, uncertainty ranges between 3.5% increases and 2.5% decreases
 336 (Fig. A7).

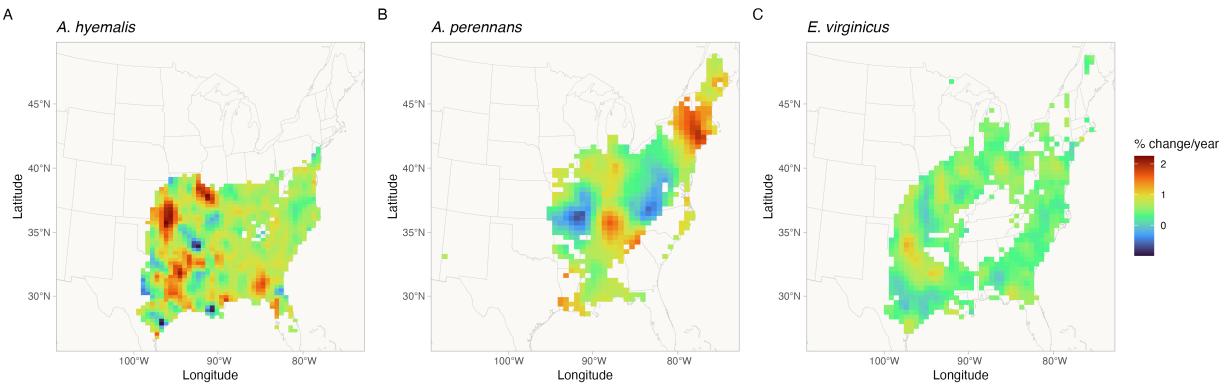


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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

339 We found that trends in endophyte prevalence were strongly associated with seasonal climate
 340 change drivers (Fig. 4). For the majority of the study region, the climate has become wetter and

341 cooler over the last century (Fig. A12-A14), a consequence of regional variation in global climate
342 change (IPCC, 2021). Within the study region, spatial variation in climate trends were predic-
343 tive of trends in endophyte prevalence. For example, strong increases in prevalence within *A.*
344 *perennans* were most associated with autumn climate drivers that coincide with its Aug-Sep active
345 growing season. For this species, warmer and wetter autumn climates showed particularly strong
346 relationships, however other seasonal drivers may also contribute to increasing endophyte preva-
347 lence (drier springs and cooler summers). Trends in endophyte prevalence for *A. hyemalis* were
348 most strongly associated with changes in precipitation variability were the strongest predictors.
349 Endophyte prevalence increased the most in regions that experienced greater spring precipita-
350 tion along with increasing variability in summer and autumn precipitation. While this species
351 actively grows and reproduces in the late spring and early summer, climate effects outside of the
352 growing season may indicate that endophytes play a role in persistence during dormant periods
353 through summer droughts or contribute to the ability to successfully germinate. Prevalence of
354 endophytes of *E. virginicus* were least influenced by climate, but decreasing autumn temperature
355 variability and less precipitation in autumn were the strongest predictors.

356 Correlations assessed using all pixels across each species distribution were qualitatively sim-
357 ilar to these results (Fig. A11).

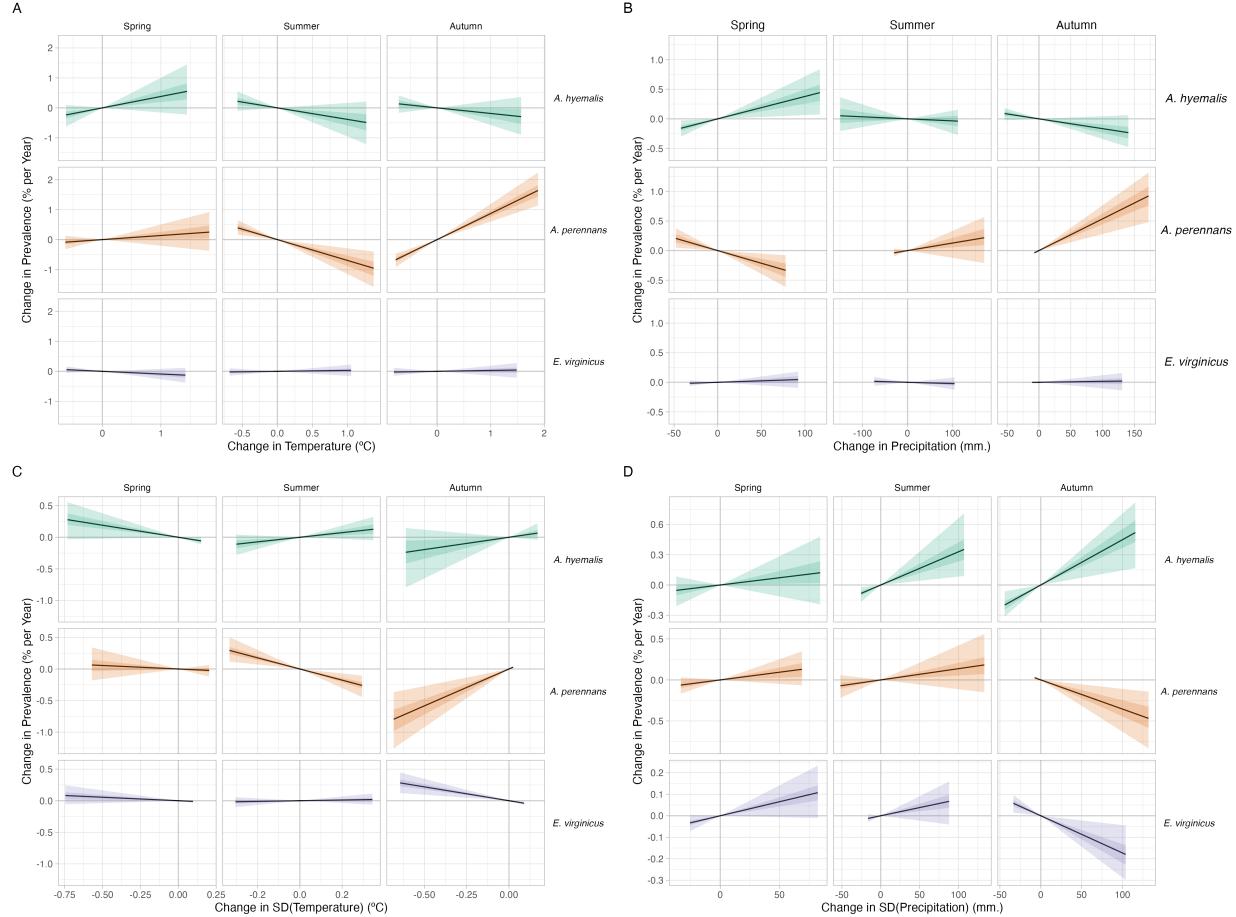


Figure 4: Relationships between changes in seasonal climate drivers and predicted marginal trends in endophyte prevalence. Lines show relationships between seasonal climate (A: mean temperature, B: cumulative precipitation, C: standard deviation in temperature, D: standard deviation in precipitation) and spatially-varying trends in endophyte prevalence for each host species, along with 50 and 95% CI.

358 *Performance on test data*

359 We found that model performance, as judged by AUC, was similar between historic herbarium
 360 specimens used as training data and the out-of-sample test data from contemporary surveys (0.79
 361 and 0.77 respectively; Fig. A5-A4). The model successfully captured broader regional trends
 362 in endophyte prevalence present in the contemporary survey data, such as decline endophyte

³⁶³ prevalence towards western longitudes in *A. hyemalis* (Fig. 5A). However, the contemporary
³⁶⁴ data contains additional variability at smaller scales not captured by our sampling of herbarium
³⁶⁵ specimens. We interpreted this to mean that the model captured regional spatial dynamics, but
³⁶⁶ underpredicts local scale dynamics. We discuss potential model improvements in the Discussion.

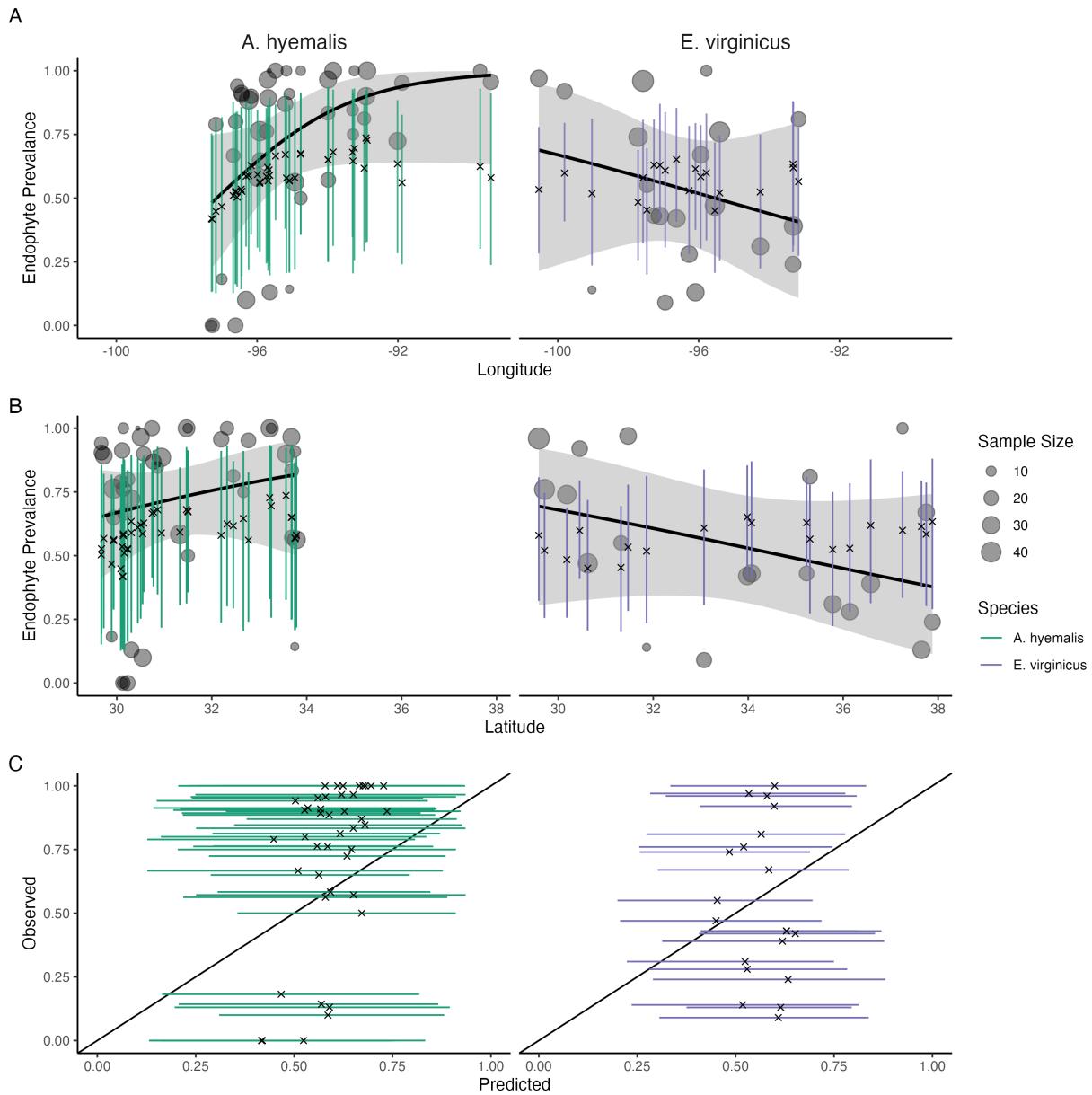


Figure 5: Predicted vs observed endophyte prevalence for contemporary test data. (A) The model, trained on historic herbarium collection data, performed modestly at predicting contemporary endophyte prevalence in *A. hyemalis*, as indicated by some overlap of predicted 95% CI with the 1:1 line, however contemporary test data generally had more variance between populations than model predictions. The model did recapitulate broader regional trends across (B) longitude and (C) latitude. Point size in panels B and C reflect sample sizes of contemporary endophyte population surveys.

367 *Assessing collector and scorer influences on predicted endophyte prevalence*

368 Our modeling effort quantified temporal and spatial trends in endophyte prevalence while ac-
369 counting for potential biases introduced by collectors and by individual scorers who quantified
370 endophyte presence/absence within specimens with the use of random effects. We found no
371 evidence that collector biases influenced our results. Collector random effects were consistently
372 small (Fig. A9), and models fit with and without this random effect provide qualitatively simi-
373 lar results. The identity of individual scorers did contribute to observed patterns in endophyte
374 prevalence. For example, 3 of the 25 scorers were more consistently likely than average to assign
375 positive endophyte status, as indicated by 95% credible intervals greater than zero) (Fig. A10).
376 This may have been driven by differences in scorers biases during the seed scoring process or
377 by unintended spatial clustering of the specimens scored by each scorer (Clayton et al., 1993;
378 Urdangarin et al., 2023). Interpreting our models with the inclusion of variance associated with
379 the scorer effect thus provides conservative estimates of the absolute magnitude of changes in
380 endophyte prevalence.

381 **Discussion**

382 Our examination of historic plant specimens revealed a cryptic biotic reponse to climate change.
383 For the three host species we examined, there have been clear increases in fungal endophyte
384 prevalence over the last two centuries. Increases in prevalence of *Epichloë*, which are vertically
385 transmitted, can potentially be interpreted as adaptive changes that improve the fitness of their
386 hosts under stressful conditions. This interpretation is in line with theory predicting that the
387 positive fitness feedback caused by vertical transmission leads beneficial symbionts to rise in
388 prevalence within a population (Fine, 1975). We found that trends in endophyte prevalence var-
389 ied across the distribution of each species in association with observed changes in climate drivers,
390 suggesting that the endophytes have contributed to host resilience under environmental change.
391 Taken together, this suggests a strengthening of the mutualism over the last two centuries.

392 Differences between the responses of each host species underscore that while all of these
393 C_3 grasses share similar broad-scale distributions, each engages in unique biotic interactions
394 and has unique niche requirements. We identified hotspots of change for *A. perennans*, which
395 experienced the strongest absolute changes in endophyte prevalence (Fig. 3). Declines in the
396 southern portion of its range and increases in the north suggest a potential poleward range shift
397 of endophytic plants. Based on previous work demonstrating that endophytes can shield their
398 hosts from drought stress (Decunta et al., 2021), we generally predicted that drought conditions
399 could be a driver of increasing endophyte prevalence. In contrast to this expectation, increasing
400 prevalence for this species was associated with increasing autumn temperature and precipitation
401 (Fig. 4). To our knowledge, the response of the symbiosis in *A. perennans* to drought has not been
402 examined experimentally, but in a greenhouse experiment, endophytes had a positive effect on
403 host reproduction under shaded, low-light conditions (Davitt et al., 2010). Our results also hint
404 that it may be useful to investigate whether lagged climate effects are important predictors of
405 host fitness in this system (Evers et al., 2021). Endophyte prevalence of the spring-flowering *A.*
406 *hyemalis* was most strongly linked to increasing variability in precipitation across summer and
407 autumn. Endophytes could be playing a role helping hosts weather autumn-season droughts
408 while the species is dormant. Previous work has demonstrated drought benefits in a greenhouse
409 manipulation with this species (Davitt et al., 2011), and early life stages may be particularly
410 vulnerable to prolonged droughts. For *E. virginicus*, which experienced the most modest changes
411 in endophyte prevalence overall, we only modest associations with changes in climate drivers.
412 Surveys by Sneck et al. (2017), used as part of the test data in this study, identified a drought index
413 (SPEI) that integrates precipitation with estimated evapotranspiration as an important predictor
414 of endophyte prevalence. *Epichloë* endophytes have also been connected to a suite of non-drought
415 related fitness benefits including herbivore protection (Brem and Leuchtmann, 2001), salinity
416 resistance (Wang et al., 2020), and mediation of the soil microbiome (Roberts and Ferraro, 2015)
417 These effects are potentially mediated by the diverse bioactive alkaloids and other signaling
418 compounds they produce (Saikonen et al., 2013). Increases in symbionts could be explained, at

419 least in part, by these diverse benefits that may help hosts weather a world made increasingly
420 stressful by changes in climate and other anthropogenically introduced stressors. While we show
421 consistent increasing trends in prevalence between the three species, the mechanisms that explain
422 these changes may be diverse and idiosyncratic.

423 Our spatially-explicit model predicted regions of both high and low endophyte prevalence,
424 suggesting that symbiotic and non-symbiotic host plants have overlapping, but non-identical
425 niche requirements. Endophytes fitness benefits potentially explain the spatial distribution of
426 prevalence by allowing their hosts to persist in environments where they otherwise could not
427 (Afkhami et al., 2014; Kazenel et al., 2015). For example, fitness benefits of the symbiosis could
428 explain historically low prevalence in *A. hyemalis* towards its western range edge coinciding with
429 a strong aridity gradient. Previous population surveys for endophytes, which were used as
430 test data for our model, found similar regional trends in prevalence for endophyte host species
431 (Rudgers and Swafford, 2009; Sneck et al., 2017). While the model recreated these large-scale
432 spatial trends, test data contained more population-to-population variability in prevalence. Val-
433 idating our model predictions in this way allows us to evaluate places to improve the model's
434 out-of-sample predictive ability, which will be particularly important for predicting host and
435 symbiont niche-shifts under future climate change. Lack of information on local variability may
436 simply be a feature of data derived from herbarium specimens. They are samples from local pop-
437 ulations, but they are single specimens that are aggregated over in broad-scale model estimates.
438 Poor predictive ability at local scales in this grass-endophyte system is not surprising, as previ-
439 ous studies have found that local variation, even to the scale of hundreds of meters can structure
440 endophyte-host niches (Kazenel et al., 2015). Other studies have found factors including land-
441 use history (Vikuk et al., 2019) and the biotic environment, including herbivory (Rudgers et al.,
442 2016), and host genotype Sneck et al. (2017), to be important predictors of endophyte ecology.
443 Incorporating available climatic and soil layers as covariates is an obvious first step that could
444 improve predictions. Another important step would be integrating data from local and regional
445 scales through modeling to constrain estimates of local and regional variation. These steps will

bridge gaps that often exist between large but broad bioclimatic and biodiversity data and small but local data on biotic interactions, and move towards the goal of predicting the dynamics of microbial symbioses under climate change (Isaac et al., 2020; Miller et al., 2019).

Our analysis advances the use of herbarium specimens in global change biology in two ways. First and foremost, this is the first study to link long-term changes in microbial symbioses to changes in climate using specimens from natural history collections. The responses of microbial symbioses are a rich target for future studies within museum specimens, particularly those that take advantage of advances in sequencing technology. While we used relatively coarse presence/absence data based on fungal morphology, other studies have examined historic plant microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these studies have so far been limited to relatively few specimens at limited spatial extents (Bieker et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al., 2015). Continued advances in capturing historic DNA and in filtering out potential contamination during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith, 2021) will be imperative in the effort to scale up these efforts. This scaling up will be essential to be able to quantify changes not just in the prevalence of symbionts, but also in symbionts' intraspecific variation and evolutionary responses to climate change, as well as in changes in the wider microbial community. Answering these questions as well as the unknown questions that future researchers may ask also reiterates the value in capturing meta-information during ongoing digitization efforts at herbaria around the world and during the accession of newly collected specimens (Edwards et al.; Lendemer et al., 2020). Second, we accounted for several potential biases in the data observation process that may be common to many collections-based research questions by using a spatially-explicit random effects model. Spatial autocorrelation (Willems et al., 2022), potential biases introduced by the sampling habits of collectors (Daru et al., 2018), and variation between contemporary researchers during the collection of trait data, if not corrected for could lead to over-confident inference about the strength and direction of historic change. Previous studies that have quantified the effects of collector biases typically find them

⁴⁷³ to be small (Davis et al., 2015; Meineke et al., 2019), and we similarly did not find that collector
⁴⁷⁴ has a strong effect on the results of our analysis.

⁴⁷⁵ Ultimately, a central goal of global change biology is to generate predictive insights into the
⁴⁷⁶ future of natural systems. While this survey of historic endophyte prevalence is necessarily cor-
⁴⁷⁷ relative, it serves as a foundation to develop better predictive models of the response of microbial
⁴⁷⁸ symbioses to climate change. Combining the insights from this type of regional-scale survey with
⁴⁷⁹ field experiments and physiological data could be invaluable. While we found that climate is
⁴⁸⁰ strongly correlated with endophytes' temporal responses, we do not know why trends in preva-
⁴⁸¹ lence were weak in some areas or how endophytes would respond to more extreme changes in
⁴⁸² climate. For example, transplanting symbiotic and non-symbiotic plants beyond the range edge
⁴⁸³ of *A. hyemalis* could tell us whether persistent low endophyte prevalence in that area is a result of
⁴⁸⁴ environmental conditions that lead the symbiosis to negative fitness consequences, or is a result
⁴⁸⁵ of some historical contingency or dispersal limitation that has thus far limited the presence of
⁴⁸⁶ symbiotic hosts from a region where they would otherwise flourish and provide resilience. While
⁴⁸⁷ we observed evidence of mutualism resilience, more extreme environmental changes than those
⁴⁸⁸ observed in our study could potentially push one or both partners beyond their physiological
⁴⁸⁹ limit, leading to the collapse of the mutualism. Our analysis thus far is agnostic to changes in the
⁴⁹⁰ distributions of hosts. Mechanistic models could connect the responses of both host and sym-
⁴⁹¹ bionts to abiotic climate drivers integrating dispersal processes. Beyond host-microbe symbioses,
⁴⁹² building these types of models would work towards quantitatively attributing biotic responses
⁴⁹³ to anthropogenically driven climate change, similar to methods in climate science and economics
⁴⁹⁴ (Carleton and Hsiang, 2016; Stott et al., 2010).

⁴⁹⁵ Acknowledgments

⁴⁹⁶ We thank Jessica Budke for help in drafting our initial destructive sampling plan, and to the
⁴⁹⁷ many members of herbarium staff who facilitated our research visits, as well as to the hundreds

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503 Program.

504 **Statement of Authorship**

505 J.C.F. contributed to research conception, data collection, data analysis, and led manuscript draft-
506 ing. J.M. contributed to data analysis and manuscript revisions. T.E.X.M. contributed
507 to research conception, data collection, data analysis, and manuscript revisions.

508 **Data and Code Availability**

509 On initial submission, you may use this section to provide a URL for editors and reviewers that
510 is 'private for peer review'. After acceptance, this section must be updated with correct, working
511 DOIs for data deposits (typically on the Dryad Digital Repository,) and code deposits (such as
512 in Zenodo).

Appendix A

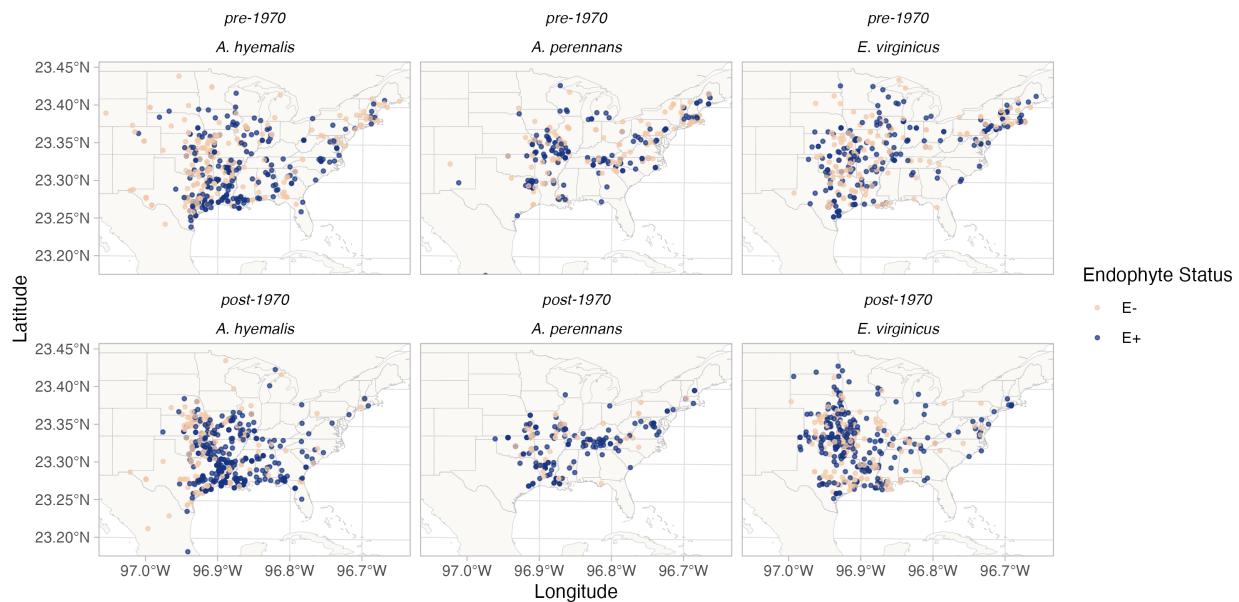


Figure A1: Endophyte presence/absence in specimens of each host species. Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points) and are faceted based on collection period.

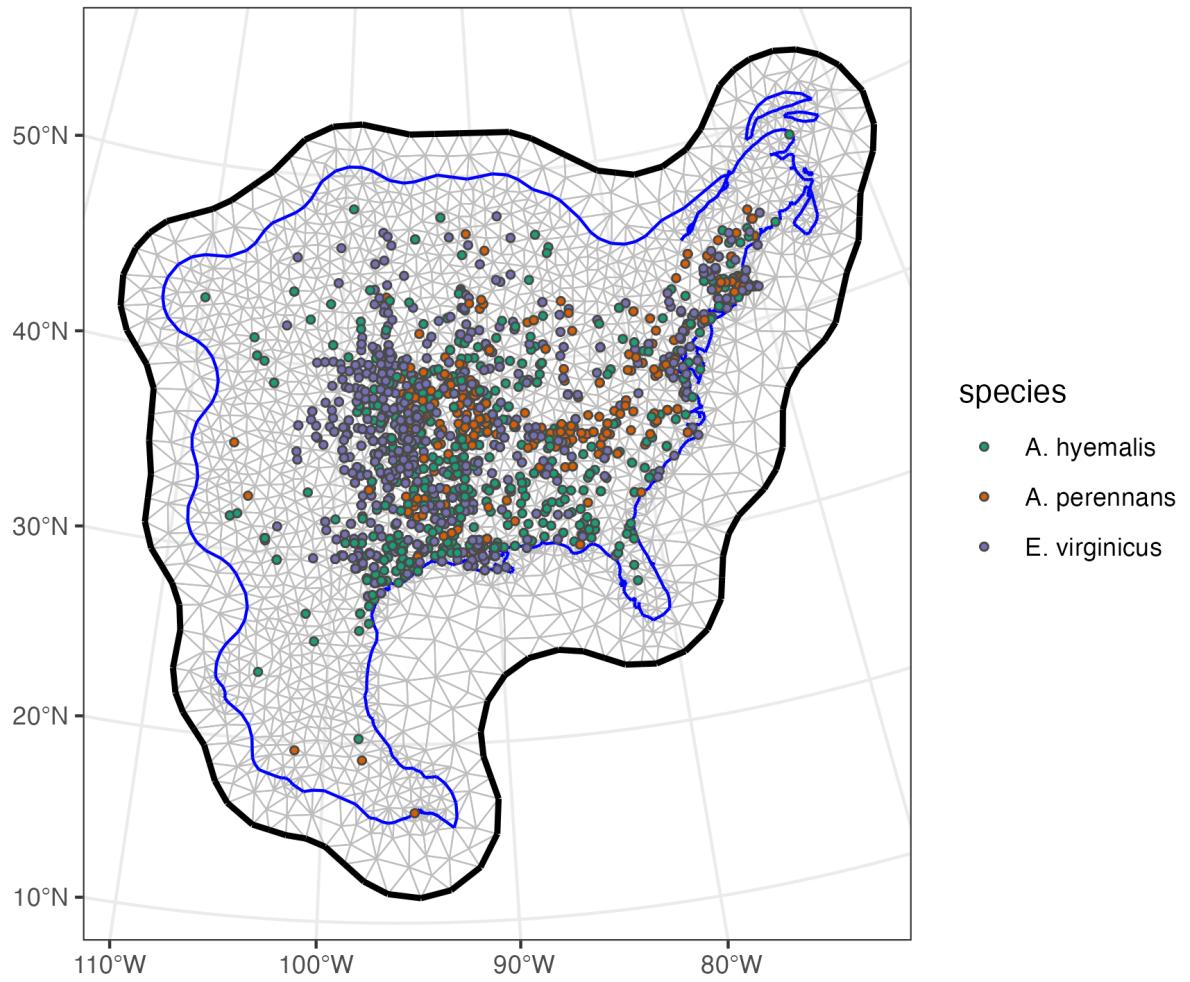


Figure A2: Triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull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

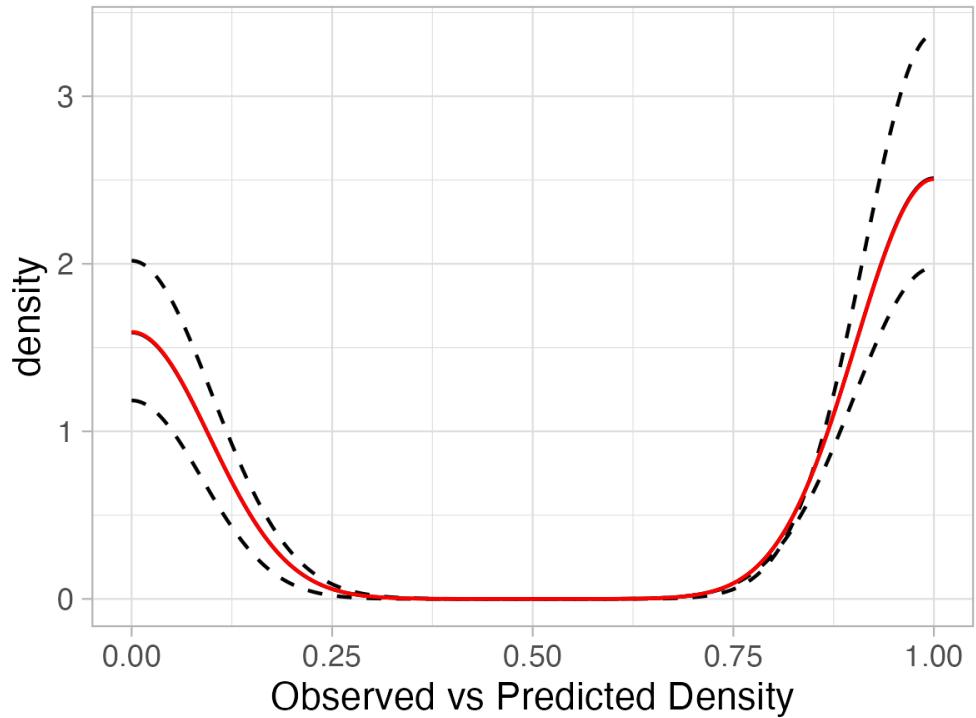


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (red) along with the mean(solid) and 95% CI (dashed) of simulated values (black).

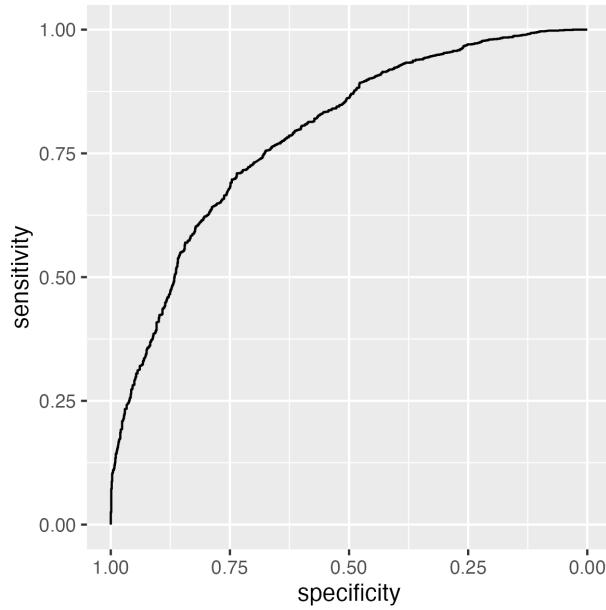


Figure A4: ROC plot showing model performance classifying observations according to endophyte status within the in-sample data. The curves show adequate model performance for observed data. The AUC value is 0.79.

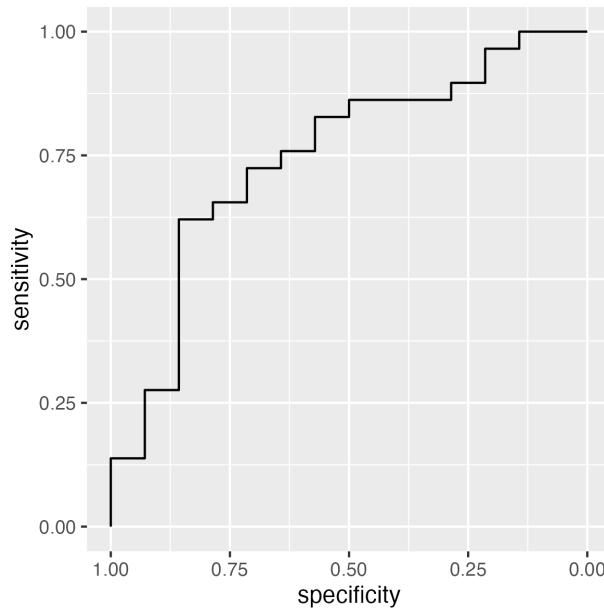


Figure A5: ROC plot showing model performance classifying observations according to endophyte status within the out-of-sample data. The curves show adequate model performance for test data. The AUC value is 0.77.

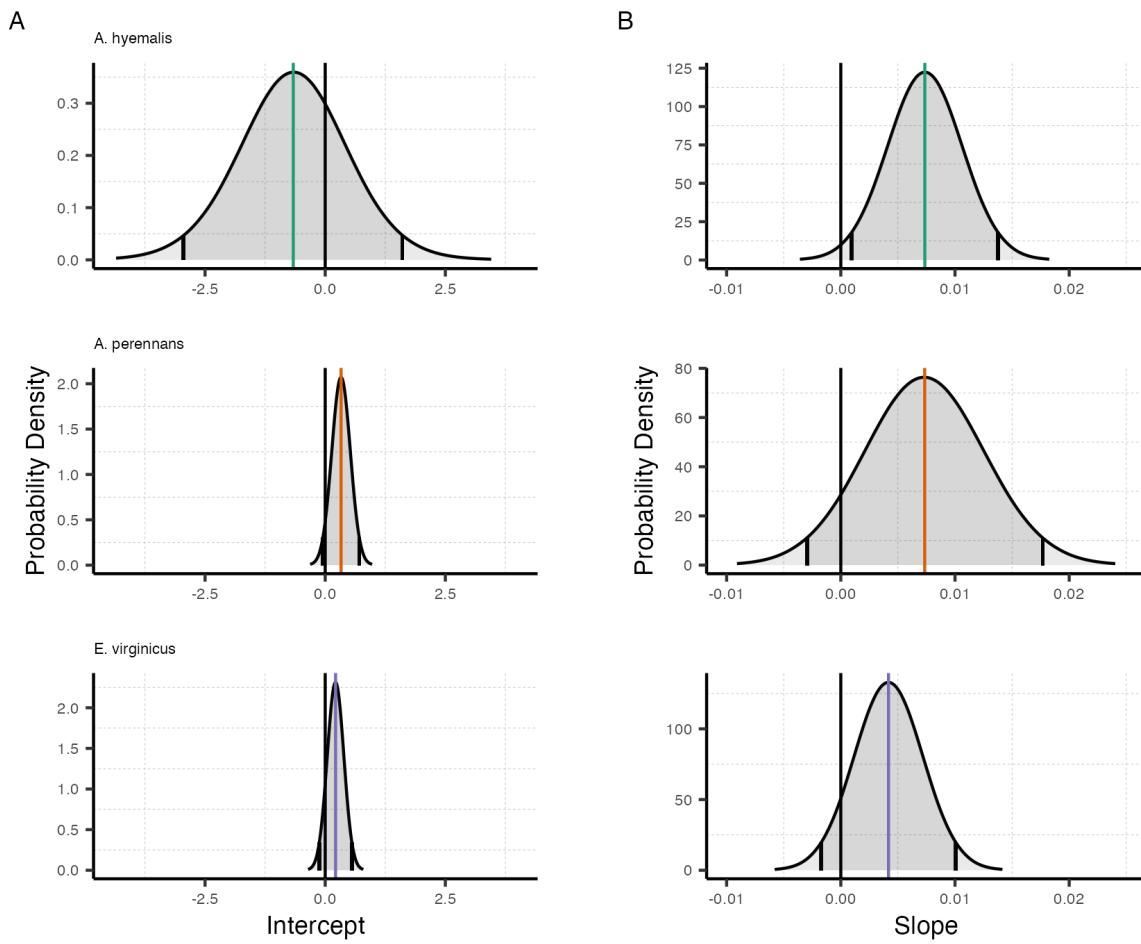


Figure A6: Density curves show the probability density along with mean (colored line) and 95% CI (black lines) for the (A) intercept and (B) slope terms, **A** and **T** respectively. Colors represent each host species

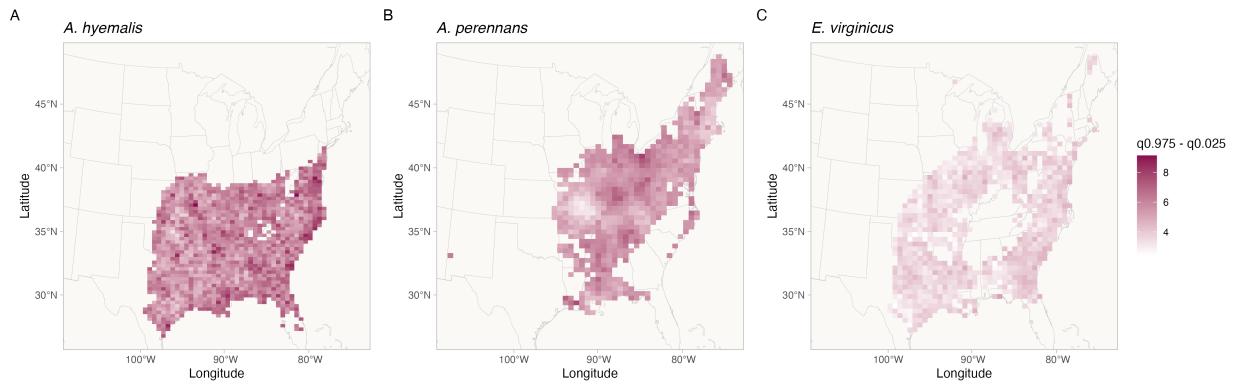


Figure A7: Shading represents the range of the 95% posterior credible interval for spatially varying slopes, τ .

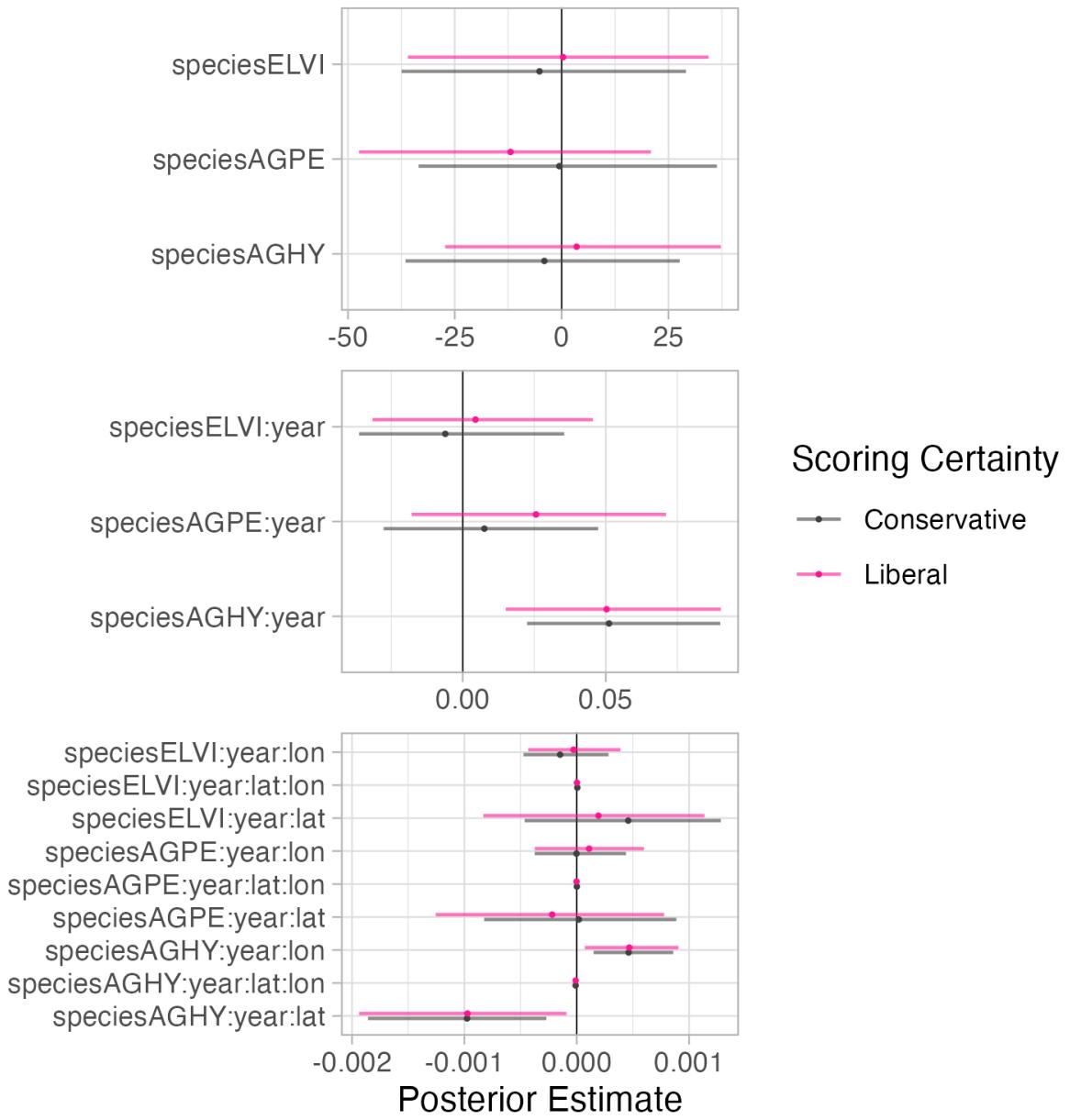


Figure A8: Comparison of posterior estimates of fixed effects when using Liberal or Conservative endophyte scores.

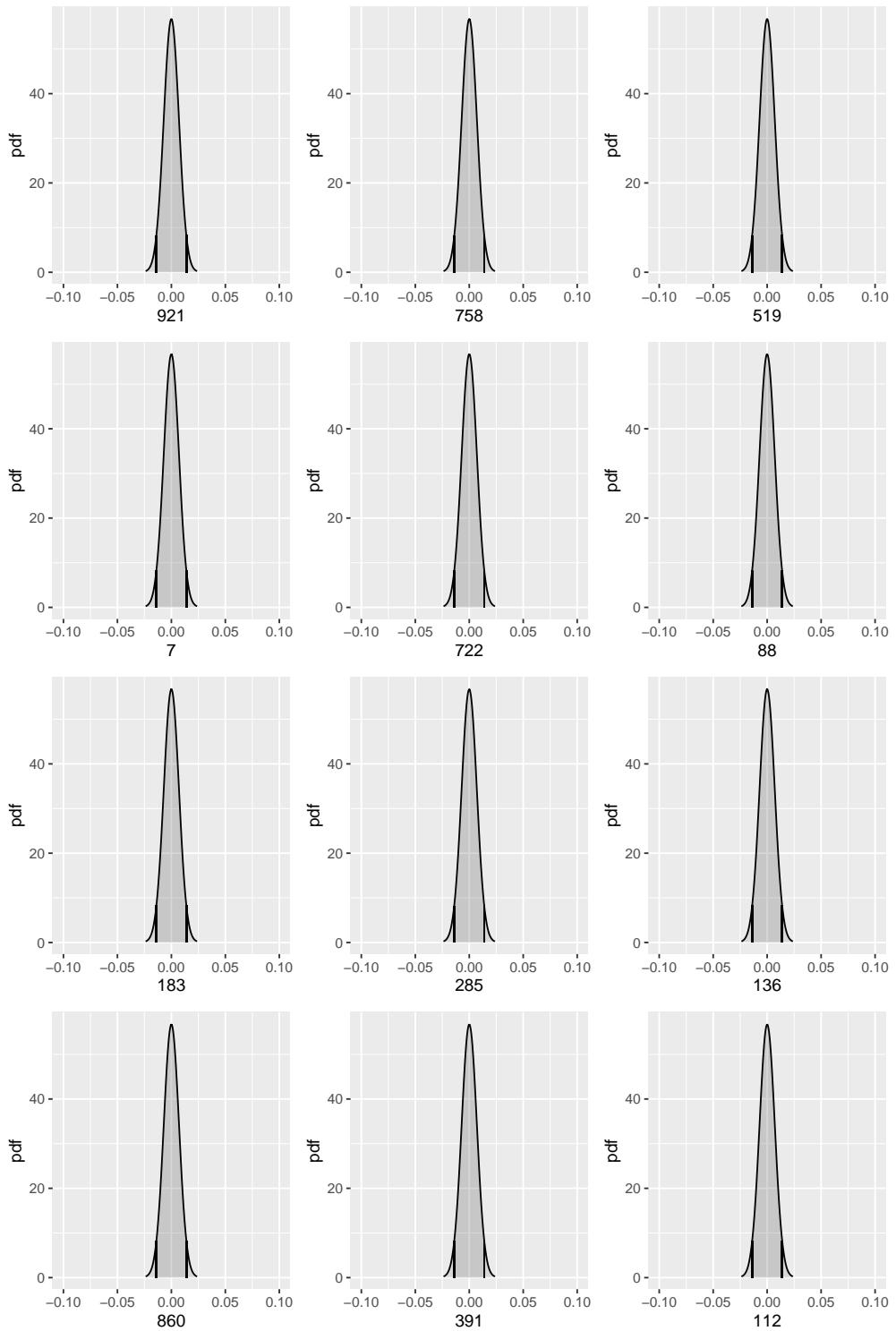


Figure A9: Posterior estimates of collector random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 12 randomly selected collectors.

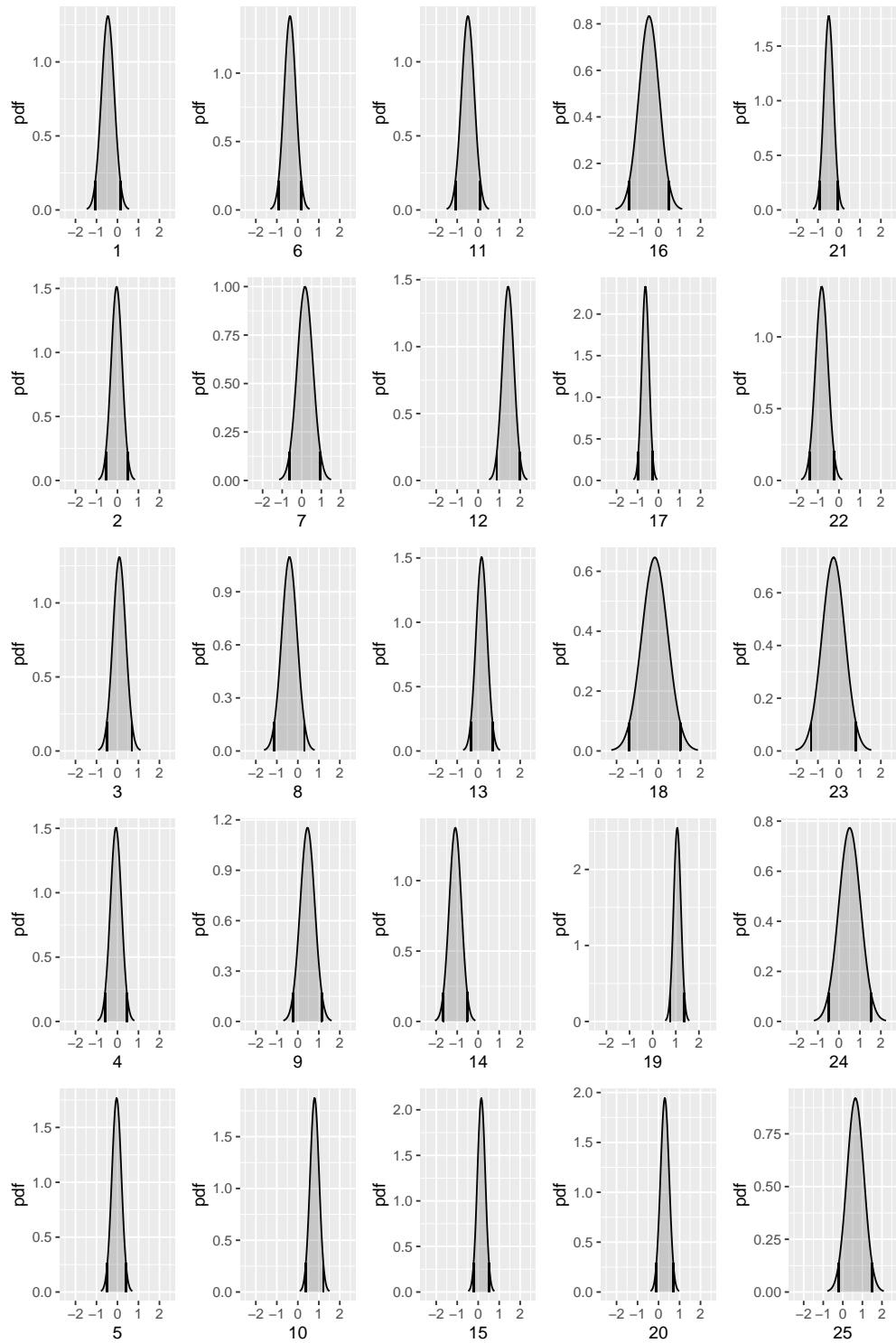


Figure A10: Posterior estimates of scorer random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 25 scorers.

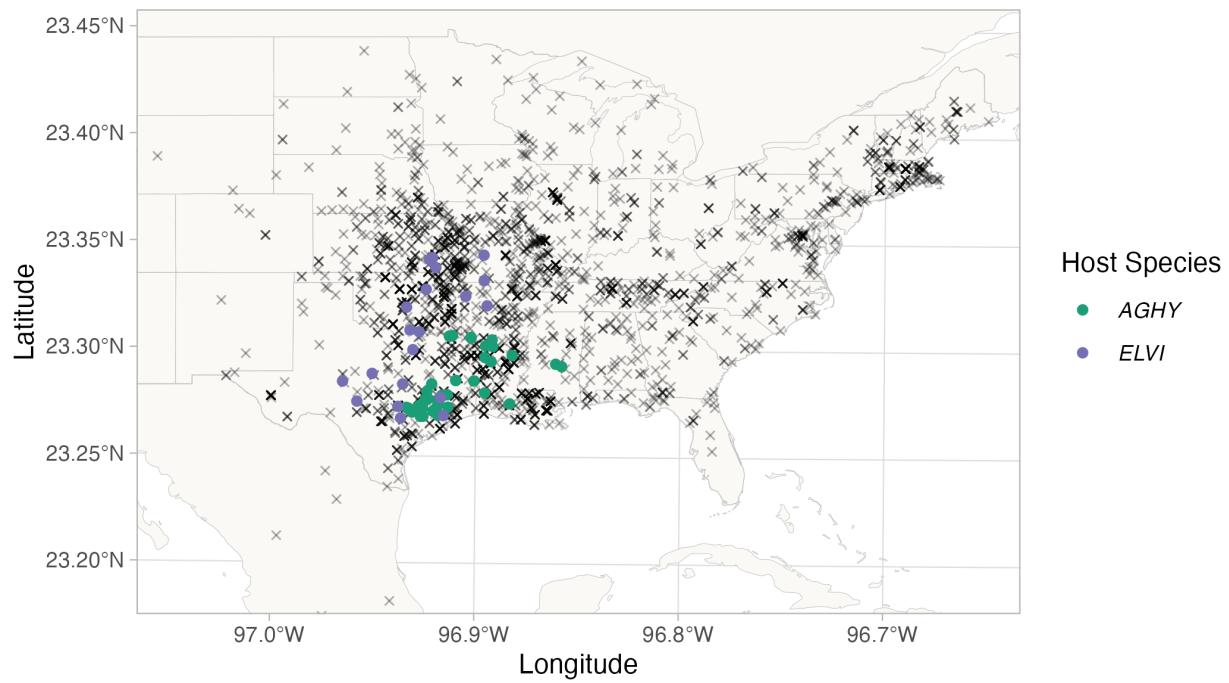
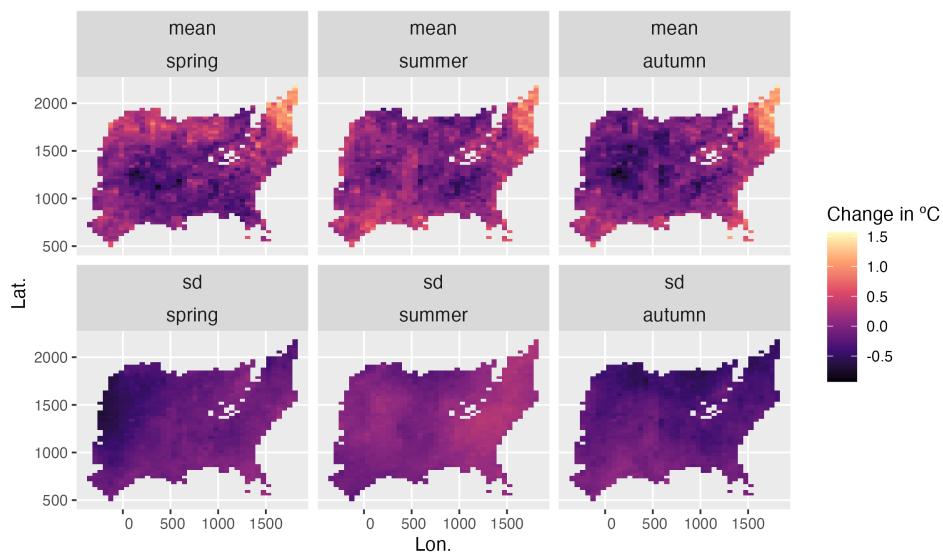


Figure A11: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

A



B

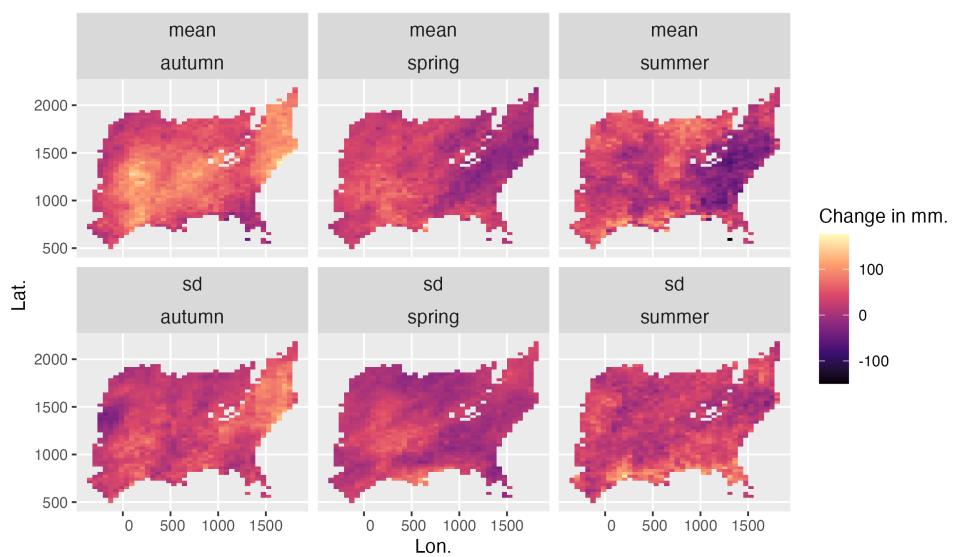
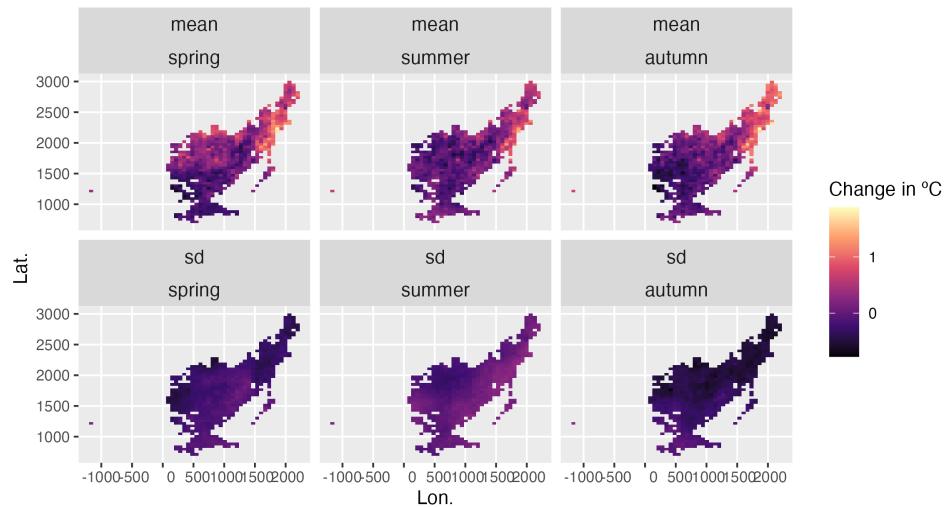


Figure A12: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. hyemalis* used in post-hoc climate correlation analysis.

A



B

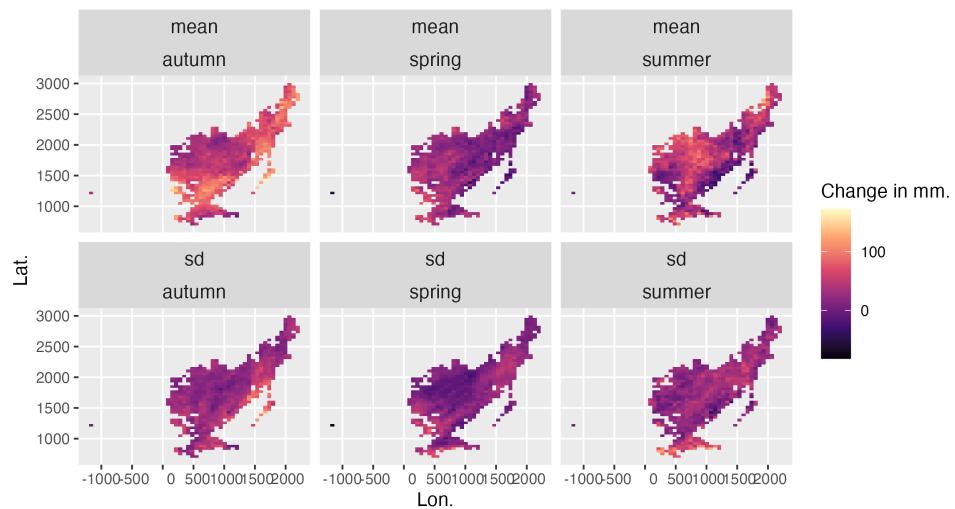


Figure A13: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020.

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.

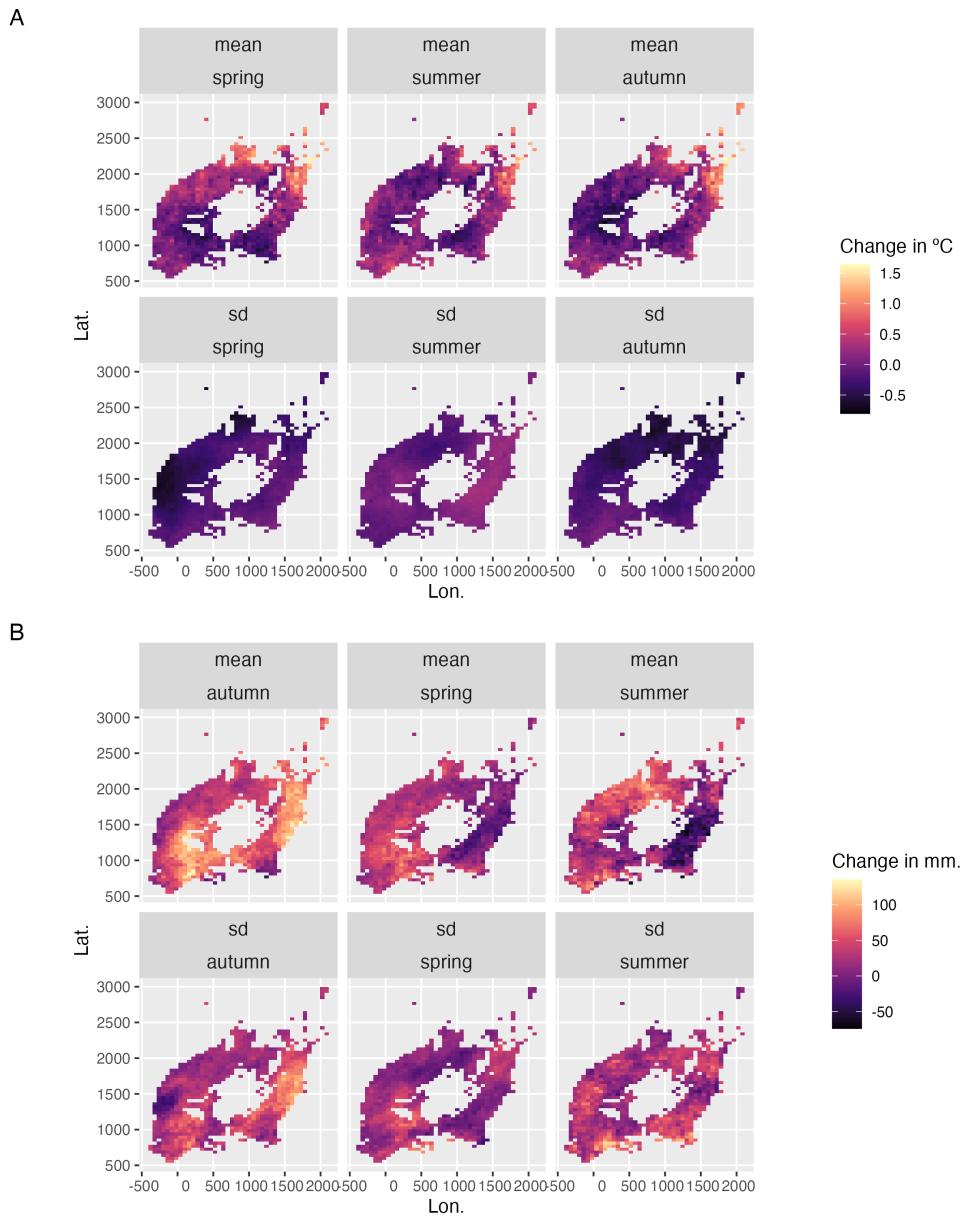


Figure A14: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *E. virginicus* used in post-hoc climate correlation analysis.

Table A1: Summary of herbarium samples across collections

Herbarium Collection	AGHY	AGPE	ELVI
Botanical Research Institute of Texas	341	189	176
Louisiana State University	71	–	61
Mercer Botanic Garden	3	–	6
Missouri Botanic Garden	78	39	31
Texas A&M	73	–	49
University of Kansas	134	–	20
University of Oklahoma	65	30	91
University of Texas & Lundell	169	41	99
Oklahoma State University	30	–	69

514

Supporting Methods

515

ODMAP Protocol

516 Overview

517 **Model purpose:** Mapping current distribution of epichloë host species.

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

519 **Study area:** United States

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

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

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

523 **Boundary:** Natural.

524 Data

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

526 ium collection across the United States. We used 713 occurrences records for *Agrostis hyemalis*,

527 656 occurrence records for *Agrostis perennans* and 2338 for *Elymus virginicus*.

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

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

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

531 [Model](#)

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

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

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

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

538 **Code availability:** Will available upon acceptance

539 **Data availability:** Will available upon acceptance

540 [Assessment](#)

541 We used AUC to test model performance.

542 [Prediction](#)

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

545

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