

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.

⁷ *Manuscript elements:* Figure 1 - Figure 5, appendix A (including Figure A1 - Figure A14, Table
⁸ A1, and Supplemental Methods).

⁹ *Keywords:* .

¹⁰ *Manuscript type:* Article.

¹¹ Prepared using the suggested L^AT_EX template for *Am. Nat.*

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 and/or symbionts. Symbionts preserved within herbarium specimens offer a unique opportunity to quantify changes in microbial symbiosis across broad temporal and spatial scales.¹ We asked how the prevalence of seed-transmitted fungal symbionts of grasses (*Epichloë* endophytes), which can protect hosts from abiotic stress, have changed over time in response to climate change, and how these changes vary across host species' ranges. Specifically, we analyzed 2,346 herbarium specimens of three grass host species (*Agrostis hyemalis*, *Agrostis perennans*, *Elymus virginicus*) collected over the past two centuries (1824 – 2019) for the presence or absence of *Epichloë* symbiosis, and evaluated spatial and temporal trends in endophyte prevalence². We found that endophytes increased in prevalence over the last two centuries from ca. 25% prevalence to ca. 75% prevalence, on average, across three host species. We also found that changes in prevalence were associated with observed changes in seasonal climate drivers; notably, increasing precipitation corresponding to each host species' peak growing season and changes in off-peak season variability in precipitation³. Our analysis performed favorably in an out-of-sample predictive test with contemporary survey data, a rare extra step in collections-based research. However, we identified greater local-scale variability in endophyte prevalence in contemporary data compared to what our model could predict based on historic data, suggesting new directions that could improve predictive accuracy. Our results provide novel evidence for a cryptic biological response to climate change that may contribute to the resilience of host-microbe symbiosis through context-dependent benefits that confer a fitness advantage to symbiotic hosts

¹If you need to cut words, I think some of this could be condensed.

²Could cut, overlaps with previous sentence.

³I would rephrase this to better communicate the sign of the association, and thus the inferred causality.

³⁶ under environmental change.

³⁷ Abstract : 287 words

Introduction

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

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

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

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

79 Understanding of how microbial symbioses are affected by climate change is additionally
80 complicated by spatial heterogeneity in the direction and magnitude of environmental change
81 (IPCC, 2021). Beneficial symbionts are likely able to shield their hosts from environmental stress
82 in locations that experience a small degree of change, but symbionts in locations that expe-
83 rience changes of large magnitude may be pushed beyond their physiological limits (Webster
84 et al., 2008). Additionally, symbionts are often unevenly distributed across their hosts' distri-
85 bution. Facultative symbionts may be absent from portions of the host range (Afkhami et al.,
86 2014), and hosts may engage with a diversity of partners (different symbiont species or locally-
87 adapted strains) across their environments (Frade et al., 2008; Rolshausen et al., 2018).⁴ Identi-
88 fying broader spatial trends in symbiont prevalence is therefore an important step in developing
89 predictions for where to expect changes in the symbiosis in future climates.

⁴I would encourage self-citation here!

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

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

¹¹⁷ to forecasting ecological dynamics into the future.

¹¹⁸ In this study, we assessed the long-term responses of endophyte symbiosis to climate change
¹¹⁹ through the use of herbarium specimens of three North American host grass species (*Agrostis*
¹²⁰ *hyemalis*, *Agrostis perennans*, and *Elymus virginicus*). We first address questions describing spa-
¹²¹ tial and temporal trends in endophyte prevalence: (i) How has endophyte prevalence changed
¹²² over the past two centuries? and (ii) How spatially variable are temporal trends in endophyte
¹²³ prevalence across eastern North America? We then address how climate change may be driv-
¹²⁴ ing trends in endophyte prevalence by asking: (iii) What is the relationship between temporal
¹²⁵ trends in endophyte prevalence and associated changes in climate drivers? We predicted that
¹²⁶ aggregate endophyte prevalence would increase over time in tandem with climate warming, and
¹²⁷ that hotspots of endophyte change would correspond spatially to hotspots of climate change.
¹²⁸ Finally, we evaluated the performance of models built on data from historic specimens with
¹²⁹ an out-of-sample test, using data on endophyte prevalence from contemporary surveys of host
¹³⁰ populations. To answer these questions we examined a total of 2,346 specimens collected across
¹³¹ eastern North America between 1824 and 2019.⁵

¹³² Methods

¹³³ Focal species

¹³⁴ Our surveys focused on three native North American grasses: *Agrostis hyemalis*, *Agrostis peren-*
¹³⁵ *nans*, and *Elymus virginicus*. Both *Agrostis* species host *Epichloë amarillans* (Craven et al., 2001;
¹³⁶ Leuchtmann et al., 2014), while *Elymus virginicus* typically hosts *Epichloë elymi* (Clay and Schardl,
¹³⁷ 2002). These C₃ grass species are commonly represented in natural history collections with broad
¹³⁸ distributions covering much the eastern United States (Fig. ??). *A. hyemalis* is a small short-lived
¹³⁹ perennial species that germinates in spring and typically flowers between March and July (most

⁵Since the preceding sentence is about the out of sample test, maybe include here the numbers of individuals and populations that the historical predictions were tested against?

¹⁴⁰ common collection month: May). *A. perennans* is of similar stature but is longer lived than
¹⁴¹ *Agrostis hyemalis* and flowers in late summer and early autumn (most common collection month:
¹⁴² September). *A. perennans* is more sparsely distributed, tending to be found in shadier and more
¹⁴³ moist habitats, while *A. hyemalis* is commonly found in open and recently disturbed ground.
¹⁴⁴ Both *Agrostis* species are recorded from throughout the Eastern US, but *A. perennans* has a slightly
¹⁴⁵ more northern distribution, whereas *A. hyemalis* is found rarely as far north as Canada and is
¹⁴⁶ listed as a rare plant in Minnesota. *E. virginicus* is a larger and relatively longer-lived species that
¹⁴⁷ is more broadly distributed than the *Agrostis* species. It begins flowering as early as March or
¹⁴⁸ April but continues throughout the summer (most common collection month: July).

¹⁴⁹ *Herbarium surveys*

¹⁵⁰ We visited nine herbaria between 2019 and 2022 (see Table A1 for a summary of specimens in-
¹⁵¹ cluded from each collection). With permission from herbarium staff, we acquired seed samples
¹⁵² from 1135 *A. hyemalis* specimens collected between 1824 and 2019, 357 *A. perennans* specimens
¹⁵³ collected between 1863 and 2017, and 854 *E. virginicus* specimens collected between 1839 and
¹⁵⁴ 2019 (Fig. 1, Fig. 2A, Fig. A1). We chose our focal species in part because they are commonly
¹⁵⁵ represented in herbarium collections, and produce high numbers of seeds, meaning that small
¹⁵⁶ samples would not diminish the value of the specimens for future studies. We collected 5-10
¹⁵⁷ seeds per specimen after examining the herbarium sheet under a dissecting microscope to en-
¹⁵⁸ sure that we collected mature seeds, not florets or unfilled seeds, fit for our purpose of identifying
¹⁵⁹ fungal endophytes with microscopy. We excluded specimens for which information about the
¹⁶⁰ collection location and date were unavailable. Each specimen was assigned geographic coor-
¹⁶¹ dinates based on collection information recorded on the herbarium sheet using the geocoding
¹⁶² functionality of the ggmap R package (Kahle et al., 2019). Many specimens had digitized collec-
¹⁶³ tion information readily available, but for those that did not, we transcribed information printed
¹⁶⁴ on the herbarium sheet. Collections were geo-referenced to the nearest county centroid, or near-
¹⁶⁵ est municipality when that information was available. **For a few of the oldest specimens, only**

¹⁶⁶ information at the state level was available, and so we used the state centroid.⁶

¹⁶⁷ After collecting seed samples, we quantified the presence or absence of *Epichloë* fungal hy-
¹⁶⁸ phae in each specimen using microscopy. We first softened seeds with a 10% NaOH solution,
¹⁶⁹ then stained the seeds with aniline blue-lactic acid stain and squashed them under a microscope
¹⁷⁰ cover slip. We examined the squashed seeds for the presence of fungal hyphae at 200-400X
¹⁷¹ magnification (Bacon and White, 2018). In some cases, the tissues examined during microscopy
¹⁷² came from flowers or otherwise non-viable seeds, which were excluded for that specimen.⁷ On
¹⁷³ average we scored 4.7 seeds per specimen of *A. hyemalis*, 4.2 seeds per specimen of *A. perennans*,
¹⁷⁴ and 3.8 seeds per specimen of *E. virginicus*; we scored 10,342 seeds in total. . Due to imper-
¹⁷⁵ fect vertical transmission (Afkhami and Rudgers, 2008), it is possible that symbiotic host-plants
¹⁷⁶ produce a mixture of symbiotic and non-symbiotic seeds. We therefore designated a specimen
¹⁷⁷ as endophyte-symbiotic if *Epichloë* hyphae were observed in one or more of its seeds, or non-
¹⁷⁸ symbiotic if *Epichloë* hyphae were observed in none of its seeds. To capture uncertainty in the
¹⁷⁹ endophyte scoring process, we recorded both a "liberal" and a "conservative" endophyte status
¹⁸⁰ for each plant specimen. When we identified potential endophytes with unusual morphology,
¹⁸¹ low uptake of stain, or a small amount of fungal hyphae across the scored seeds, we recorded a
¹⁸² positive liberal status (more likely to be endophyte-positive) and a negative conservative status
¹⁸³ (less likely to be endophyte-positive). 89% of scored plants had matching liberal and conservative
¹⁸⁴ scores, reflecting high confidence in endophyte status. The following analyses used the liberal
¹⁸⁵ status, but we repeated all analyses with the conservative status which yielded qualitatively
¹⁸⁶ similar results (Fig. A8).

¹⁸⁷ Modeling spatial and temporal changes in endophyte prevalence

¹⁸⁸ We assessed spatial and temporal changes in endophyte prevalence across each host distribution,
¹⁸⁹ quantifying the "global" temporal trends aggregated across space, and then examining spatial

⁶ Say how many?

⁷ Could cut, since you already say you only took good seeds.

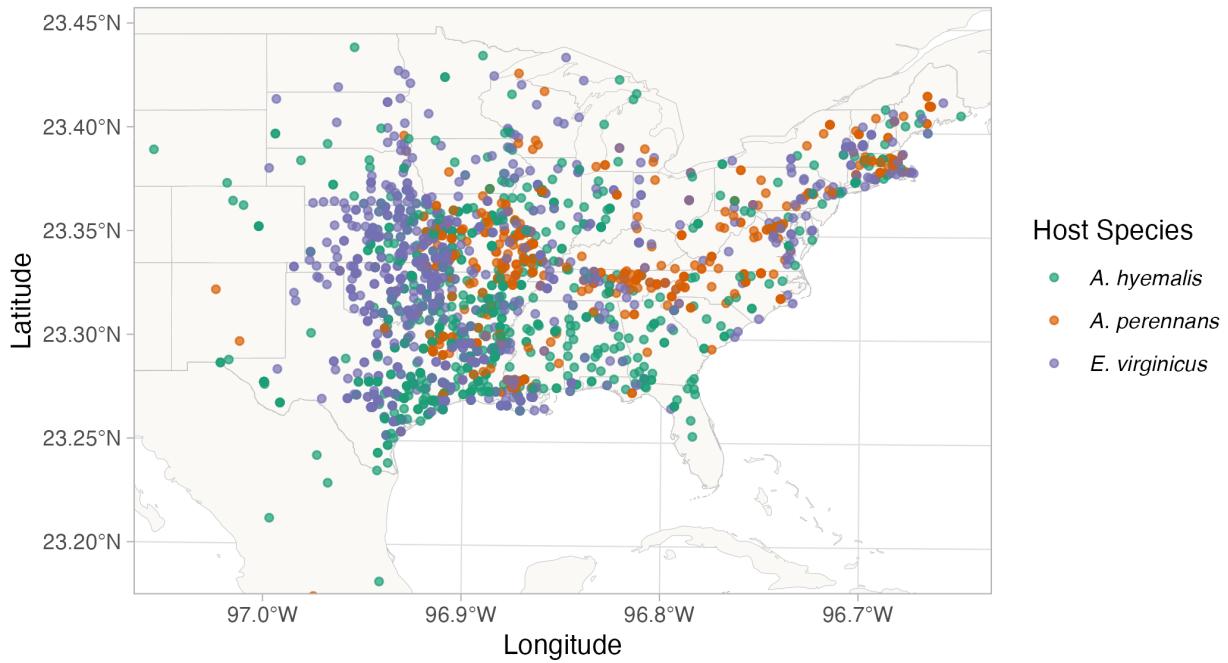


Figure 1: Collection locations of herbarium specimens of three grass host species across eastern North America that were sampled for *Epichloë* endophyte presence or absence.

190 heterogeneity in the direction and magnitude of endophyte change (hotspots and coldspots)
 191 across the spatial extent of each host's distribution. To account for the spatial non-independence
 192 of geo-referenced occurrences, we used an approximate Bayesian method, Integrated Nested
 193 Laplace Approximation (INLA), to construct spatio-temporal models of endophyte prevalence.
 194 INLA provides a computationally efficient method of ascertaining parameter posterior distribu-
 195 tions for certain models that can be formulated as latent Gaussian Models (Rue et al., 2009).
 196 Many common statistical models, including structured and unstructured mixed-effects models,
 197 can be represented as latent Gaussian Models. We incorporated spatial heterogeneity into this
 198 analysis using spatially-structured intercept and slope parameters implemented as stochastic
 199 partial differential equations (SPDE) to approximate a continuous spatial Gaussian process. This
 200 SPDE approach is a flexible method of smoothing across space while explicitly accounting for
 201 spatial dependence between data-points (Bakka et al., 2018; Lindgren et al., 2011). Fitting models

202 with structured spatial effects is possible with MCMC sampling but can require long computa-
 203 tion times, making INLA an effective alternative. This approach has been used to model spatial
 204 patterns in flowering phenology (Willems et al., 2022), the abundance of birds (Meehan et al.,
 205 2019) and butterflies (Crossley et al., 2022), the distribution of temperate trees (Engel et al., 2022)
 206 as well as the population dynamics of endangered amphibians (Knapp et al., 2016) and other
 207 ecological processes (Beguin et al., 2012).⁸

208 We estimated global and spatially-varying trends in endophyte prevalence using a joint-
 209 likelihood model. For each host species h , endophyte presence/absence of the i^{th} specimen ($P_{[h]i}$)⁹
 210 was modeled as a Bernoulli response variable with expected probability of endophyte occurrence
 211 $\hat{P}_{[h]i}$. We modeled $\hat{P}_{[h]i}$ as a linear function of intercept $A_{[h]i}$ ¹⁰ and slope $T_{[h]}$ defining the global
 212 trend in endophyte prevalence specific to each host species as well as with spatially-varying
 213 intercepts $\alpha_{[h_1]l[i]}$ and slopes $\tau_{[h_1]l[i]}$ associated with location ($l[i]$, the unique latitude-longitude
 214 combination of the i^{th} observation). The joint-model structure allowed us to “borrow strength”
 215 across species in the estimation of shared variance terms for the spatially-dependent random ef-
 216 fect $\delta_{l[i]}$, intended to account for residual spatial variation, and $\chi_{c[i]}$ and $\omega_{s[i]}$ i.i.d.-random effects
 217 indexed for each collector identity ($c[i]$), and scorer identity ($s[i]$) of the i^{th} specimen.¹¹

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

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

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

218 By including random effects for collectors and scorers, we accounted for “nuisance” variance
 219 that may bias predictions for changes in endophyte prevalence. Previous work suggests that
 220 behavior of historical botanists may introduce biases into ecological inferences made from historic

⁸Probably not necessary if you need space.

⁹Not obvious to me why you use square brackets here.

¹⁰I don't think there should be an i subscript here. You need i only where there is a covariate unique to the i^{th} observation.

¹¹I don't think you need three expressions here. If you just index host as h it is clear that some pieces are unique to host h and others are shared across hosts.

221 collections (Kozlov et al., 2020). Prolific collectors who contribute thousands of specimens may
222 be more or less likely to collect certain species, or specimens with certain traits (Daru et al., 2018).
223 Similarly, the process of scoring seeds for hyphae involved several student researchers who, even
224 with standardized training, may vary in their likelihood of positively identifying *Epichloë*.

225 We performed model fitting using the inlabru R package (Bachl et al., 2019). Global intercept
226 and slope parameters A, and T, were given vague priors. Scorer and collector random effects,
227 χ and ω , were given penalized complexity priors, with distributions approximating a Normal
228 distribution with standard deviation of 5. Each spatially-structured parameter depended on a
229 covariance matrix according to the proximity of each pair of collection locations (Bakka et al.,
230 2018; Lindgren et al., 2011). The covariance matrix was approximated using a Matérn covariance
231 function, with each data point assigned a location according to the nodes of a mesh of non-
232 overlapping triangles encompassing the study area (Fig. A2). We assessed model fit with visual
233 posterior predictive checks (A3) and measurements of AUC (Figs. A4-A5). Priors for the Matérn
234 covariance function, termed "range" and "variance", define how proximity effects decay with
235 distance. Priors for results presented in the main text reflect a range of 342 kilometers. We
236 found that model results were somewhat sensitive to the choices of priors for these parameters,
237 so we tested a range of values (from 68 kilometers to 2160 kilometers) and meshes (Supplemental
238 Material), finding that model results were qualitatively similar, i.e. the same direction of effects
239 across space, but that the magnitude and uncertainty varied.¹²

¹²I struggled here. I tried to make some edits but I don't think I understand the methods well enough to edit correctly. It is not clear how the distances you quote should be interpreted (locations within 68 or 2160 km are more likely to have the same endo status just due to proximity?), or whether they should be interpreted at all. The text seems to say both the priors do not matter, but also that they do. I have not looked at what is in the supplement yet, but if you present results there based on different priors it should be easy to write this in a way that succinctly says "priors mattered a little bit, and if you care you can look at the supplement for a prior sensitivity analysis."

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

241 We evaluated the predictive ability of the model using both in-sample training data from the
242 herbarium surveys, and with out-of-sample test data, an important but rarely used strategy in
243 ecological studies (Lee et al., 2024; Tredennick et al., 2021). We generated out-of-sample test
244 data from contemporary surveys of endophyte prevalence in natural populations of *A. hyemalis*
245 and *E. virginicus* in Texas and the southern US. Surveys of *E. virginicus* were conducted in 2013
246 as described in Sneck et al. (2017), and surveys of *A. hyemalis* took place between 2015 and
247 2020. Population surveys of *A. hyemalis* were initially designed to cover longitudinal variation
248 in endophyte prevalence towards its range edge, while surveys of *E. virginicus* were designed to
249 cover latitudinal variation. In total, we visited 43 populations of *A. hyemalis* and 20 populations
250 of *E. virginicus* across the south-central US, with emphasis on Texas and neighboring states (Fig
251 A11). During surveys, we collected seeds from up to 30 individuals per population (average
252 number of plants sampled per population: 22.9); note that this sampling design provided greater
253 local depth of information than the herbarium records, where only one plant was sampled at
254 each locality. We quantified the endophyte status of each individual with staining microscopy
255 as described for the herbarium surveys (with 5-10 seeds scored per individual), and calculated
256 the prevalence of endophytes within the population (proportion of plants that were endophyte-
257 symbiotic). For each population, we compared the observed fraction of endophyte-symbiotic
258 hosts to the predicted probability of endophyte occurrence \hat{P} derived from the model for that
259 location and year. The contemporary survey period (2013-2020) is at the most recent edge of the
260 time period encompassed by the historical observations used for model fitting.

261 *Assessing the role of climate drivers*

262 We assessed how the magnitude of climate change may have driven changes in endophyte preva-
263 lence by assessing correlations between changes in climate and changes in endophyte prevalence
264 predicted from our spatial model at evenly spaced pixels across the study area. We first down-

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

283 To evaluate whether areas that have experienced the greatest changes in endophyte preva-
284 lence (hotspots of endophyte change) are associated with high degrees of change in climate
285 (hotspots of climate change), we modeled the fitted, spatially-varying slopes of endophyte change
286 through time ($\tau_{[h]l}$) as a linear function of environmental covariates, with a Gaussian error dis-
287 tribution.¹³ Data from each host species was analyzed separately. Fitting regressions to many
288 pixels across the study region risks artificially inflating confidence in our results due to large sam-
289 ple sizes, and so we performed this analysis using only a random subsample of 250 pixels across

¹³If I am reading the results figure correctly it looks like you force an intercept of zero, and I am not sure why you would want to do that.

290 the study region; other sizes of subsample yielded similar results.

291 *Modeling distributions of host species*

292 Because the herbarium records did not encompass the entirety of these host species' ranges,
293 we additionally modeled the geographic distribution of each host species to generate realistic
294 maps on which we could project the predictions of the INLA model. We followed the ODMAP
295 (overview, data, model, assessment, prediction) protocol (Crossley et al., 2022) (see Supporting
296 Methods). In short, we used presence-only observations of each host species from Global Biodi-
297 versity Information Facility (GBIF) **between 1990 to 2020**¹⁴. We fit maximum entropy (MaxEnt)
298 models using the maxent function in the R package dismo (Hijmans et al., 2017) using the same
299 set of seasonal climate predictors considered above: **mean and standard deviation of spring,**
300 **summer, and autumn temperature, and mean and standard deviation of spring, summer, and**
301 **autumn cumulative precipitation.**¹⁵ We generated 10,000 pseudo-absences as background points,
302 and split the occurrence data into 75% for model training and 25% for model testing. The perfor-
303 mance of models was evaluated with AUC (Jiménez-Valverde, 2012). **We found AUC values of**
304 **0.862, 0.838, 0.821 respectively for *Agrostis hyemalis*, *Agrostis perennans*, and *Elymus virginicus*.**¹⁶ To
305 convert the continuous predicted probabilities into binary presence - absence maps on which we
306 projected INLA predictions, we used the training sensitivity (true positive rate) and specificity
307 threshold (true negative rate) (Liu et al., 2005).

¹⁴I am not sure why 1990-2020. From our conversations, I thought the SDM was based on all records. At this point I would not change anything.

¹⁵Were these 1990-2020 normals?

¹⁶Can we make this sentence more evaluative? I think AUC > 0.8 is very good, yes?

Results

309 *How has endophyte prevalence changed over time?*

310 Across >2300 herbarium specimens dating back to 1824, we found that prevalence of *Epichloë*
311 endophytes increased over the last two centuries for all three grass host species (Fig. 2). On
312 average, endophytes of *A. perennans* and *E. virginicus* increased from ~ 40 % to 70% prevalence
313 across the study region, and *A. hyemalis* increased from ~ 25% to over 50% prevalence. Our
314 model indicates a high certainty that overall temporal trends are positive across species (99%
315 probability of a positive overall year slope in *A. hyemalis*, 92% probability of a positive overall
316 year slope in *A. perennans*, and 91% probability of a positive overall year slope in *E. virginicus*)
317 (Fig. A6). The model appears to under-predict the observed increase in endophyte prevalence
318 relative to the data, particularly for *A. hyemalis* (Fig. 2A), but the model is accounting for random
319 effects and spatial non-independence that are not readily seen in the figure. By under-weighting
320 endophyte-positive samples that are clustered spatially or by collector or observer, the INLA
321 model is appropriately accounting for nuisance variables and providing a conservative inference
322 of endophyte change relative to the raw data.

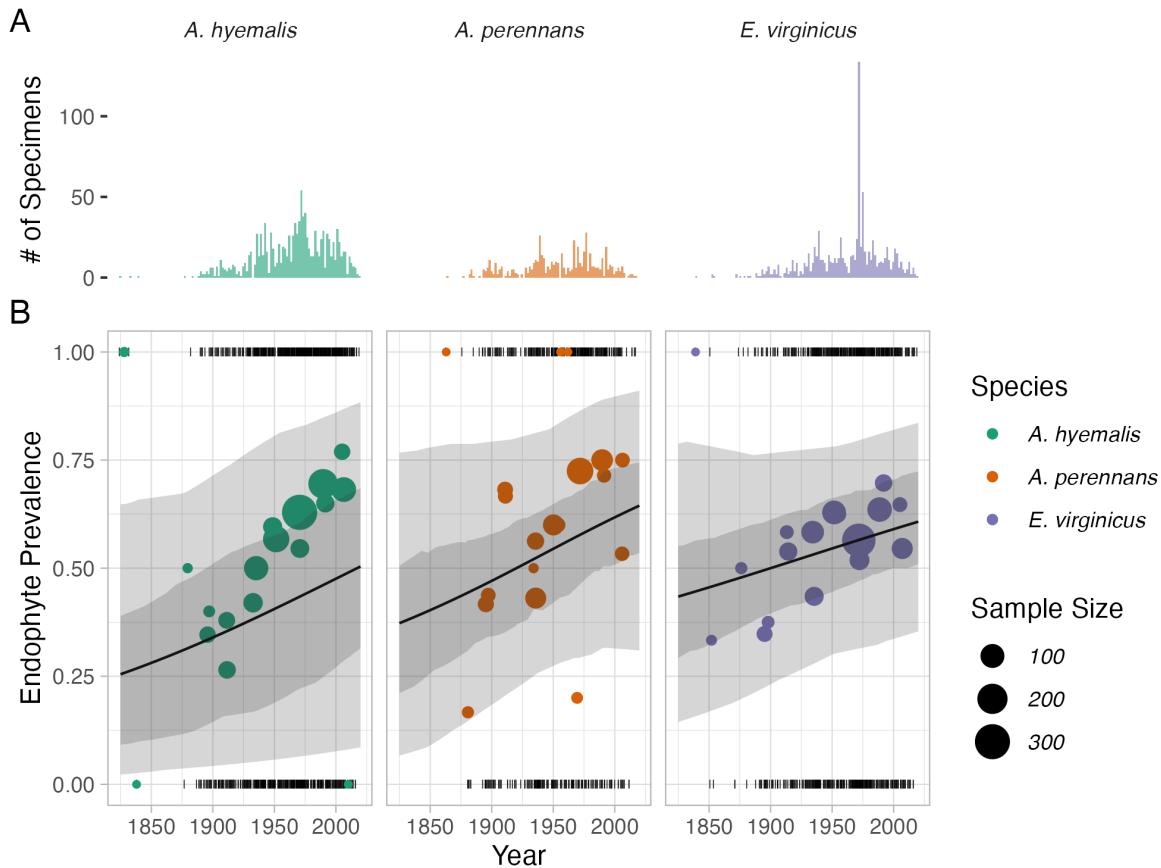


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of scored specimens through time for each host species. (B) Lines show predicted mean endophyte prevalence over the study period along with the 50% and 95% CI bands incorporating uncertainty associated with collector 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 While there was an overall increase in endophyte prevalence, our model revealed hotspots and
 325 coldspots of change across the host species' ranges, which are mapped in Fig. 3 across geographic
 326 ranges predicted by MaxEnt species distribution models. In some regions, posterior mean esti-

327 mates of spatially varying temporal trends indicate that *A. hyemalis* and *A. perennans* experienced
 328 increases in prevalence by as much as 2% per year over the study period, while *E. virginicus* expe-
 329 rienced increases up to around 1% per year. Both *Agrostis* species show areas of strong increase
 330 and areas of declining prevalence, while *E. virginicus* had an overall weaker and geographically
 331 more consistent increase in endophyte prevalence. Notably, endophytes increased most strongly
 332 towards the western range edge of *A. hyemalis* (Fig. 3A) and across the northeastern US for *A.*
 333 *perennans* (Fig. 3B). Posterior estimates of uncertainty in spatially varying slopes indicate that
 334 these hotspots of change may have experienced increases of up to 5% per year while declines
 335 in prevalence may be as great as 4% per year for *A. hyemalis* and *A. perennans*. For *E. virginicus*,
 336 uncertainty ranges between 3.5% increases and 2.5% decreases (Fig. A7).

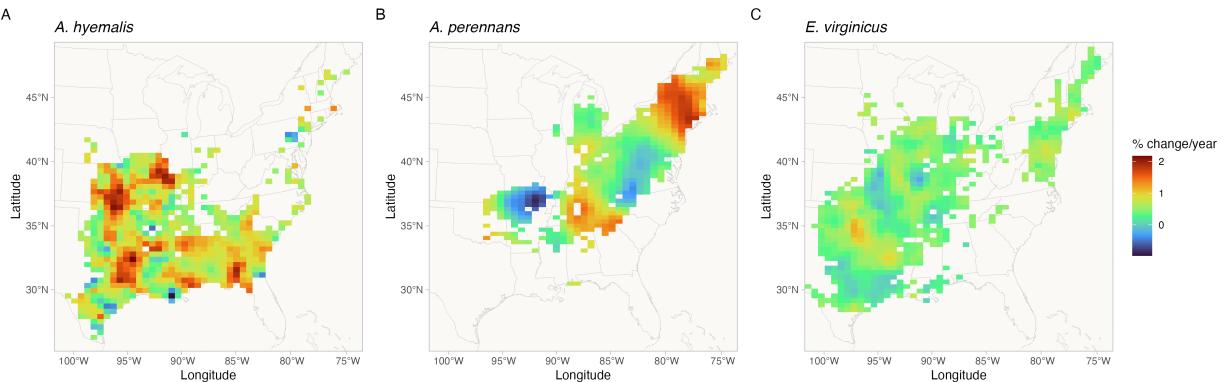


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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

339 ¹⁷ 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**¹⁸ (Fig. A12-A14), a consequence of regional variation in global climate
342 change (IPCC, 2021).¹⁹ Spatial variation in climate trends were predictive of trends in endophyte
343 prevalence. For example, strong increases in endophyte prevalence for *A. perennans* were most
344 strongly associated with change in autumn climate drivers that coincide with its active growing
345 season.²⁰ For this species, regions experiencing warmer and wetter autumn climates showed
346 particularly strong relationships with increasing endophyte prevalence, however other seasonal
347 drivers may also contribute (drier springs and cooler summers). Trends in endophyte prevalence
348 for *A. hyemalis* were most strongly associated with changes in precipitation and precipitation
349 variability. Endophyte prevalence in *A. hyemalis* increased the most in regions that experienced
350 greater increases in spring precipitation, as well as regions with changing variability in spring
351 and autumn precipitation. **Changes in endophyte prevalence in *E. virginicus* were not strongly**
352 **associated with changes in most climate drivers**²¹, but regions of reduced variability in autumn
353 precipitation were associated with weak reductions in prevalence. **Correlations**²² assessed using
354 all pixels across each species' distribution were qualitatively similar to these results (Fig. A11).

¹⁷I think this section would be strengthened by greater statistical support. It is really just eye-balling lines. Can we say something more quantitative? See my comment about posteriors of slopes – that is the type of information I have in mind, and maybe we could embed some of this in the text.

¹⁸Can you provide the average change in degrees celsius and mm precip across the range?

¹⁹Comment on these supplement figures: perhaps for the revision, I think a color scale that diverges at zero would be helpful here.

²⁰Here and throughout the results, please reference specific figures and panels for statements like this so readers can see what you see. Regarding the figure, since it is just a bunch of regression lines and we only care about the slopes, it might be more effective to just show posteriors of the slopes - probably not worth making that change at this point, and maybe it's ugly.

²¹Notice that my edits here importantly change the meaning of the sentence and, as far as I understand, make it more correct.

²²I am not sure why you describe these as "correlations". The methods makes these sound like linear regressions.

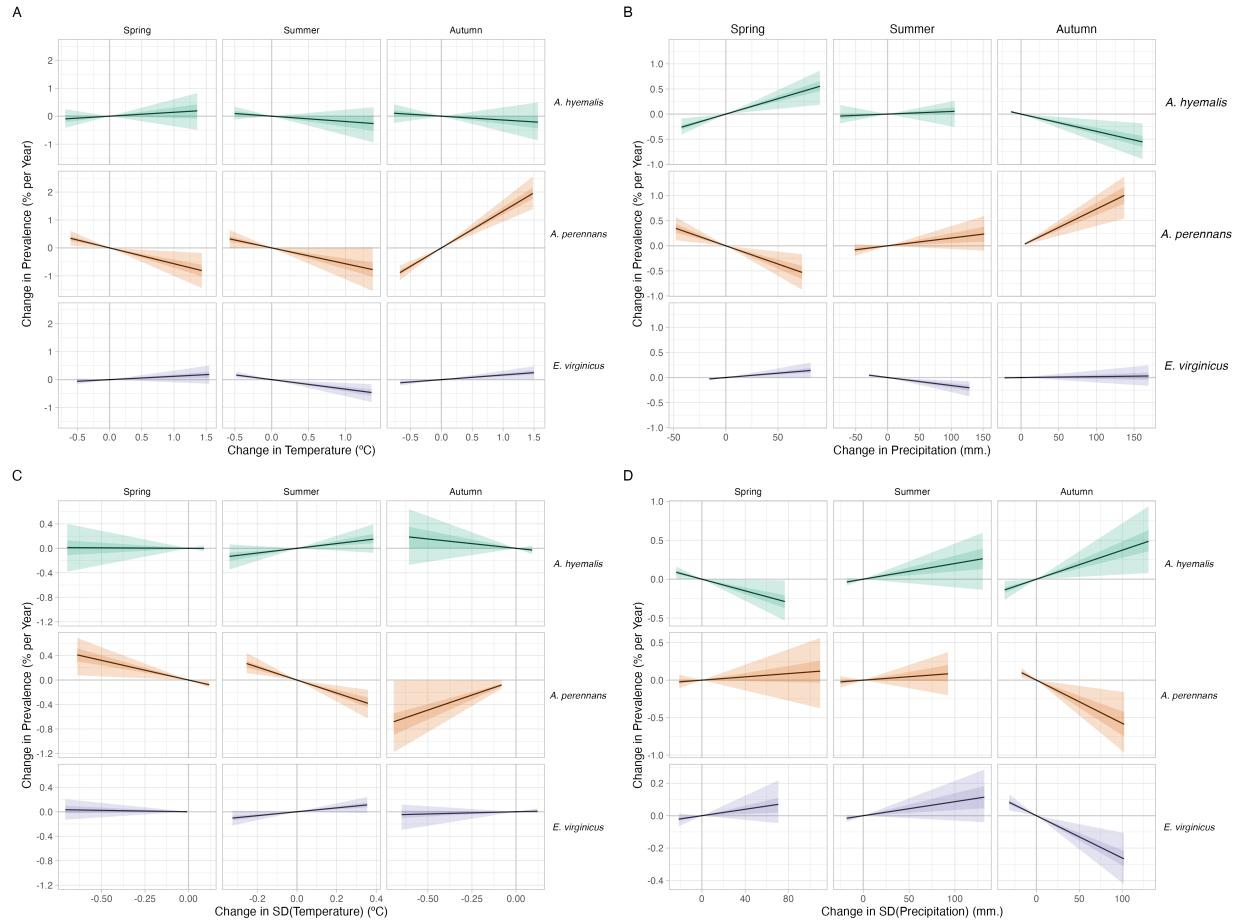


Figure 4: Relationships between changes in seasonal climate drivers and predicted marginal trends in endophyte prevalence. Lines show relationships between seasonal climate (A: mean temperature, B: cumulative precipitation, C: standard deviation in temperature, D: standard deviation in precipitation)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

355 Performance on test data

356 ²³ We found that model performance, as quantified by AUC, was similar between historic herbarium specimens used as training data and the out-of-sample test data from contemporary surveys
 357 (0.79 and 0.77 respectively; Fig. A5-A4). The model successfully captured broad regional trends

²³The order of the results does not match the order of the methods.

359 in endophyte prevalence seen in the contemporary survey data, such as decline endophyte preva-
360 lence in *A. hyemalis* towards western longitudes (Fig. 5A) and northern latitudes (Fig. 5B). How-
361 ever, model predictions for endophyte prevalence exhibited relatively little geographic variation,
362 whereas the out-of-sample survey data were maximally variable with populations spanning 0%
363 to 100% endophyte-symbiotic plants (Fig. 5C)²⁴. We interpret this to mean that the model cap-
364 tures coarse-scale spatial and temporal trends reasonably well, but is not equipped to capture
365 local-scale nuances that generate population-to-population differences.

²⁴*Love the figure but I think the legend can be improved. It does not describe the content very well.*

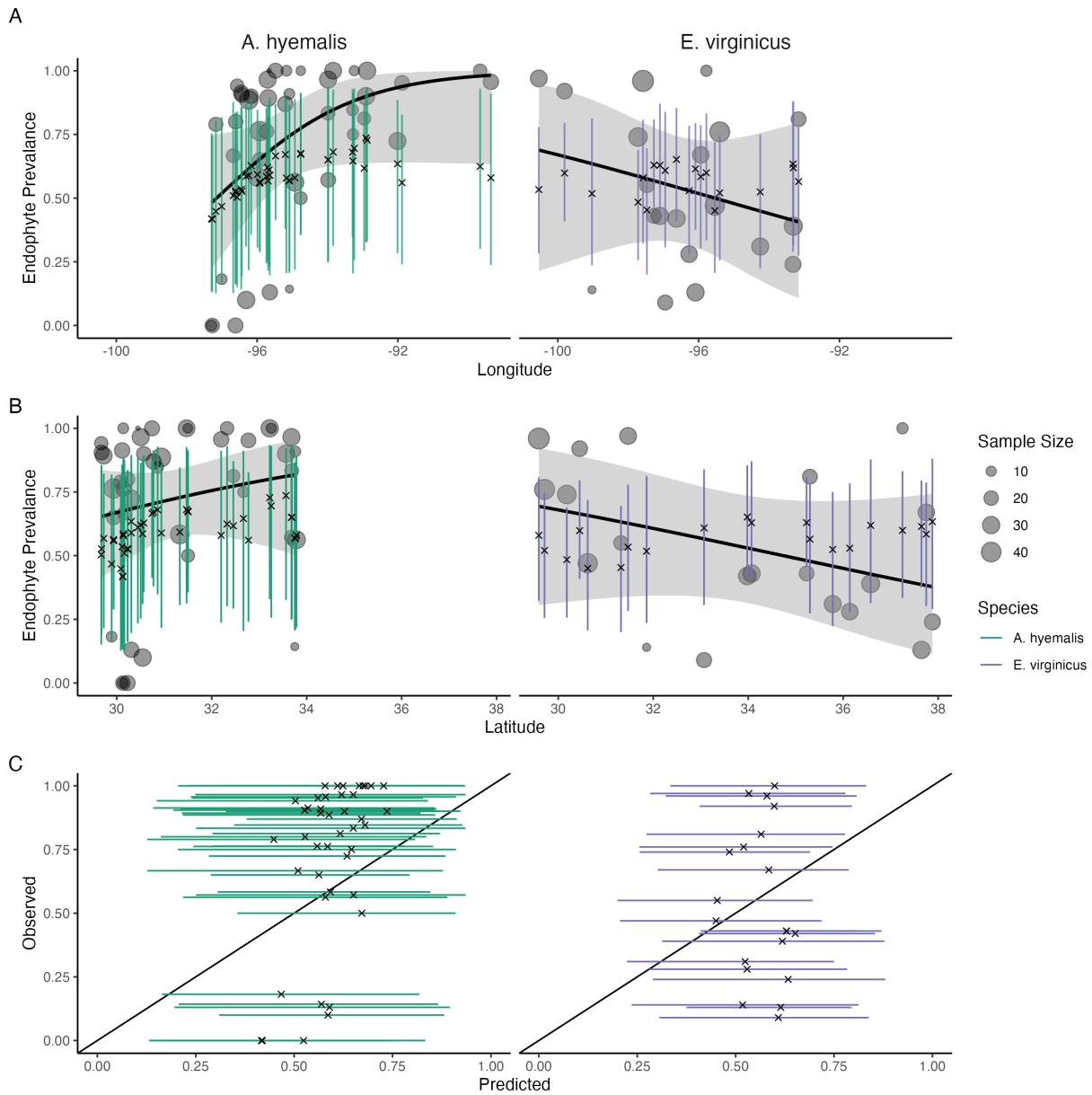


Figure 5: Predicted vs observed endophyte prevalence for contemporary test data. (A) The model, trained on historic herbarium collection data, performed modestly at predicting contemporary endophyte prevalence in *A. hyemalis*, as indicated by some overlap of predicted 95% CI with the 1:1 line, however 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.

366 Assessing collector and scorer influences on predicted endophyte prevalence

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

Discussion

381 Our examination of historic plant specimens revealed cryptic shifts in microbial symbiosis over
382 the last two centuries. For the three host species we examined, there have been strong increases
383 in prevalence of fungal endophytes. We interpret increases in prevalence of *Epichloë*, which are
384 vertically transmitted, as adaptive changes that improve the fitness of their hosts under increas-
385 ing environmental stress. This interpretation is in line with theory predicting that the positive
386 fitness feedback caused by vertical transmission leads beneficial symbionts to rise in prevalence
387 within a population (Donald et al., 2021; Fine, 1975). We further found that trends in endophyte
388 prevalence varied across the distribution of each species in association with changes in climate
389 drivers, suggesting that the increases in endophyte prevalence are driven by context-dependent
390 benefits to hosts that confer resilience under environmental change. Taken together, this suggests

391 an overall strengthening of host-symbiont mutualism over the last two centuries.

392 Differences across host species underscore that while all of these C_3 grasses share similar
393 broad-scale distributions, each engages in unique biotic interactions and has unique responses to
394 environmental drivers. We identified hotspots of change for *A. perennans*, which was the species
395 that experienced the strongest absolute changes²⁵ in endophyte prevalence (Fig. 3). Declines in
396 the southern portion of its range and increases in the north suggest a potential poleward range
397 shift of endophyte-symbiotic plants (whether the overall host distribution is shifting in parallel
398 is an exciting next question). Based on previous work demonstrating that endophytes can shield
399 their hosts from drought stress (Decunta et al., 2021)²⁶, we generally predicted that drought con-
400 ditions would be a driver of increasing endophyte prevalence. In contrast to this expectation,
401 increasing prevalence for this species²⁷ was associated with increasing autumn temperature and
402 precipitation (Fig. 4). To our knowledge, the response of the symbiosis in *A. perennans* to drought
403 has not been examined experimentally, but in a greenhouse experiment, endophytes had a pos-
404 itive effect on host reproduction under shaded, low-light conditions (Davitt et al., 2010). Our
405 results also hint that it may be useful to investigate whether lagged climate effects are important
406 predictors of host fitness in this system (Evers et al., 2021). Endophyte prevalence of the spring-
407 flowering *A. hyemalis* was most strongly linked to increasing variability in precipitation across
408 summer and autumn.²⁸ Endophytes could be playing a role helping hosts weather autumn-
409 season droughts while the species is dormant.²⁹ Previous work has demonstrated drought
410 benefits in a greenhouse manipulation with this species (Davitt et al., 2011), and early life stages

²⁵remind readers what the absolute change was

²⁶I would cite this as "reviewed in" or something like that, so this is not read as a single case study

²⁷I have now forgotten which species you are talk about, since the previous sentence is about grass-endophyte interactions more generally. I think this paragraph can be edited to make it clearer which are general statements and which refer to specific species (and which ones).

²⁸I do not see this in the figure. I would argue you are over-interpreting the SD effects. The ppt amount effects look stronger, and these are in autumn and spring which lines up with this species' growing season. Marion's paper showed that wet autumn conditions can neutralize the benefits of the symbiosis, which I think is consistent with your result.

²⁹Not dormant in autumn. They probably start germinating in October.

may be particularly vulnerable to prolonged droughts. For *E. virginicus*, which experienced the most modest changes in endophyte prevalence overall, we only modest associations with changes in climate drivers. Surveys by Sneck et al. (2017), used as part of the test data in this study, identified a drought index (SPEI) that integrates precipitation with estimated evapotranspiration as an important predictor of endophyte prevalence. *Epichloë* endophytes have also been connected to a suite of non-drought related fitness benefits including herbivore protection (Brem and Leuchtmann, 2001), salinity resistance (Wang et al., 2020), and mediation of the soil microbiome (Roberts and Ferraro, 2015). These effects are potentially mediated by the diverse bioactive alkaloids and other signaling compounds they produce (Saikkonen et al., 2013). Increases in symbionts could be explained, at least in part, by these diverse benefits that may help hosts weather a world made increasingly stressful by changes in climate and other anthropogenically introduced stressors. While we show consistent increasing trends in prevalence between the three species, the mechanisms that explain these changes may be diverse and idiosyncratic.³⁰

Our spatially-explicit model predicted regions of both high and low endophyte prevalence, suggesting that symbiotic and non-symbiotic host plants have overlapping, but non-identical niche requirements.³¹ Endophytes fitness benefits potentially explain the spatial distribution of prevalence by allowing their hosts to persist in environments where they otherwise could not (Afkhami et al., 2014; Kazenel et al., 2015)³². For example, fitness benefits of the symbiosis could

³⁰This paragraph was a little hard to read and I think does not really nail the points that I think we should make here, IMO. I would open to paragraph setting up the idea that the correlations you detected have some support in previous experimental studies, then elaborate. Then I would acknowledge that other factors can elicit benefits of symbiosis, and these factors may ALSO be changing. The takeaway, for me and perhaps for readers more generally, is that we are very confident endophytes are increasing, we have some confidence that is associated with (and perhaps due to) climate change, but a lot has changed over the past 200 years (climate, urbanization, nitrogen deposition, invasive species, deer!) and we need follow-up studies and experiments to gain a better mechanistic understanding of what has driven these changes, which will also allow us to build better forecasts about the future.

³¹I think this paragraph tries to do too much relative to this topic sentence. In general I think you could use stronger topics sentences to give these Discussion paragraphs greater focus.

³²cite Eco Monograph

429 explain historically low prevalence in *A. hyemalis* towards its western range edge coinciding
430 with a strong aridity gradient.³³ Previous population surveys for endophytes found similar
431 regional trends in prevalence for endophyte host species (Rudgers and Swafford, 2009; Sneck
432 et al., 2017)³⁴. While the model recreated the large-scale spatial trends observed in contemporary
433 population surveys, test data contained more population-to-population variability in prevalence.
434 Validating our model predictions in this way, a rare extra step in collections-based studies, allows
435 us to evaluate places to improve the model's out-of-sample predictive ability, which will be
436 particularly important for predicting host and symbiont niche-shifts under future climate change.
437 Lack of information on local variability may simply be a feature of data derived from herbarium
438 specimens. They are samples from local populations, but they are single specimens that are
439 aggregated to derive broad-scale model estimates. Poor predictive ability at local scales in this
440 grass-endophyte system is not surprising, as previous studies have found that local variation,
441 even to the scale of hundreds of meters can structure endophyte-host niches (Kazenel et al.,
442 2015). Other studies have found factors including land-use history (Vikuk et al., 2019) and the
443 biotic environment, including herbivory (Rudgers et al., 2016), and host genotype Sneck et al.
444 (2017), to be important predictors of endophyte ecology. Incorporating available climatic and soil
445 layers as covariates is an obvious first step that could improve predictions.³⁵ Another important
446 step would be integrating data from local and regional scales through modeling to constrain
447 estimates of local and regional variation. These steps will bridge gaps that often exist between
448 large but broad bioclimatic and biodiversity data and small but local data on biotic interactions,
449 and move towards the goal of predicting the dynamics of microbial symbioses under climate
450 change (Isaac et al., 2020; Miller et al., 2019).

451 Our analysis advances the use of herbarium specimens in global change biology in two ways.

³³But above you say that AGHY gets benefits under drought.

³⁴I would add the semimartin study.

³⁵This is not where my mind went. I was thinking more local replication/redundancy, e.g. multiple specimens from the same population. Your idea is getting at explaining the local variation, but right now the model is not even seeing the local variation because we (rightly I think) prioritized larger-scale geographic coverage.

452 First and foremost, this is the first study to link long-term changes in microbial symbioses to
453 changes in climate using specimens from natural history collections. The responses of micro-
454 bial symbioses are a rich target for future studies within museum specimens, particularly those
455 that take advantage of advances in sequencing technology.³⁶ While we used relatively coarse
456 presence/absence data based on fungal morphology, other studies have examined historic plant
457 microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these
458 studies have so far been limited to relatively few specimens at limited spatial extents (Bieker
459 et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al.,
460 2015). Continued advances in capturing historic DNA and in filtering out potential contamina-
461 tion during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith, 2021)
462 will be imperative in the effort to scale up these efforts. This scaling up will be essential to
463 be able to quantify changes not just in the prevalence of symbionts, **but also in symbionts' in-**
464 **traspecific variation and evolutionary responses to climate change**³⁷, as well as in changes in the
465 wider microbial community. Answering these questions as well as the unknown questions that
466 future researchers may ask also reiterates the value in capturing meta-information during ongo-
467 ing digitization efforts at herbaria around the world and during the accession of newly collected
468 specimens (Edwards et al.; Lendemer et al., 2020). Second, we accounted for several potential
469 biases in the data observation process that may be common to many collections-based research
470 questions by using a spatially-explicit random effects model. Spatial autocorrelation (Willem's
471 et al., 2022), potential biases introduced by the sampling habits of collectors (Daru et al., 2018),
472 and variation between contemporary researchers during the collection of trait data, if not cor-
473 rected for could lead to over-confident inference about the strength and direction of historic
474 change (I would cite the AGHY figure as an example). **Previous studies that have quantified the**

³⁶*This is not the place for it, but this sentence made me think about genetic variation in the endophytes. We see presence-absence changing but the endophytes themselves could also be changing ("chemotypes") which is something we could possibly detect if we could get fungal DNA out of the samples. Maybe worth mentioning this somewhere.*

³⁷*OK maybe this is the place for it. I would add a sentence about how endophytes can vary by chemotype and different chemotypes can confer different benefits.*

475 effects of collector biases typically find them to be small (Davis et al., 2015; Meineke et al., 2019),
476 and we similarly did not find that collector has a strong effect on the results of our analysis.³⁸

477 Ultimately, a central goal of global change biology is to generate predictive insights into the
478 future of natural systems on a rapidly changing planet. While this survey of historic endophyte
479 prevalence is necessarily correlative, it serves as a foundation to develop better predictive mod-
480 els of the response of microbial symbioses to climate change. Combining the insights from this
481 type of regional-scale survey with field experiments and physiological data **could be invaluable.**³⁹ While we found that certain dimensions of climate change were strongly correlated
482 with endophytes' temporal responses, we do not know why trends in prevalence were weak
483 in some areas or how endophytes would respond to more extreme changes in climate. **For ex-**
484 **ample, transplanting symbiotic and non-symbiotic plants beyond the range edge of *A. hyemalis***
485 **could tell us whether persistent low endophyte prevalence in that area is a result of environ-**
486 **mental conditions that lead the symbiosis to negative fitness consequences, or is a result of some**
487 **historical contingency or dispersal limitation that has thus far limited the presence of symbi-**
488 **otic hosts from a region where they would otherwise flourish and provide resilience.**⁴⁰ While
489 the "time machine" of natural history collections revealed evidence of mutualism resilience for
490 grass-endophyte symbioses in the face of environmental change, more extreme changes could
491 potentially push one or both partners beyond their physiological limits, leading to the collapse of
492 the mutualism; more research is needed to understand what those limits might be. **Our analysis**
493 **thus far is agnostic to changes in the distributions of hosts. Mechanistic models could connect**
494 **the responses of both host and symbionts to abiotic climate drivers, integrating dispersal pro-**

³⁸ This seems to undercut the previous sentence, but its also a place where you could mention that scorer effects DID matter, so this is worth incorporating when possible.

³⁹ Vague.

⁴⁰ This does not fit well here. I would move earlier where you talk about geographic trends. I also want to highlight that there is an important difference between associations of endophyte prevalence and geographic variation in climate (as in this AGHY example), and associations between CHANGES in endophyte prevalence and CHANGES in climate (the lines figure). Too often the manuscript blurs this distinction, and it happens here.

496 cesses.⁴¹ Beyond host-microbe symbioses, building these types of models would work towards
497 quantitatively attributing biotic responses to anthropogenically driven climate change, similar to
498 methods in climate science and economics (Carleton and Hsiang, 2016; Stott et al., 2010).⁴²

499

Acknowledgments

500 We thank Dr. Jessica Budke for help in drafting our initial destructive sampling plan, and to the
501 many staff members of herbaria who facilitated our research visits, as well as to the hundreds
502 of collectors who contributed to the natural history collections. Several high schooler and un-
503 dergraduate researchers contributed to data collection, including A. Appio-Riley, P. Bilderback,
504 E. Chong, K. Dickens, L. Dufresne, B. Gutierrez, A. Johnson, S. Linder, E. Scales, B. Scherick,
505 K. Schrader, E. Segal , G. Singla, and M. Tucker. This research was supported by funding from
506 National Science Foundation (grants 1754468 and 2208857) and by funding from the Texas Ecolab
507 Program.

508

Statement of Authorship

509 J.C.F. contributed to research conception, data collection, data analysis, and led manuscript draft-
510 ing. J.M. contributed to data analysis and manuscript revisions. T.E.X.M. contributed to research
511 conception, data collection, data analysis, and manuscript revisions.

512

Data and Code Availability

513 Data from this publication will be made publically available upon acceptance and before that
514 upon request.⁴³ Code for analyses can be found through a publicly available repository (<https://github.com/josh>)
515 that will be permanently archived upon publication.

⁴¹Does not feel like it fits well as a concluding point.

⁴²Not knowing these citations, I am not really sure what you are referring to. This does not feel like a natural point to end on.

⁴³CHeck journal requirements. It is generally better to make data and code available during peer review.

Appendix A

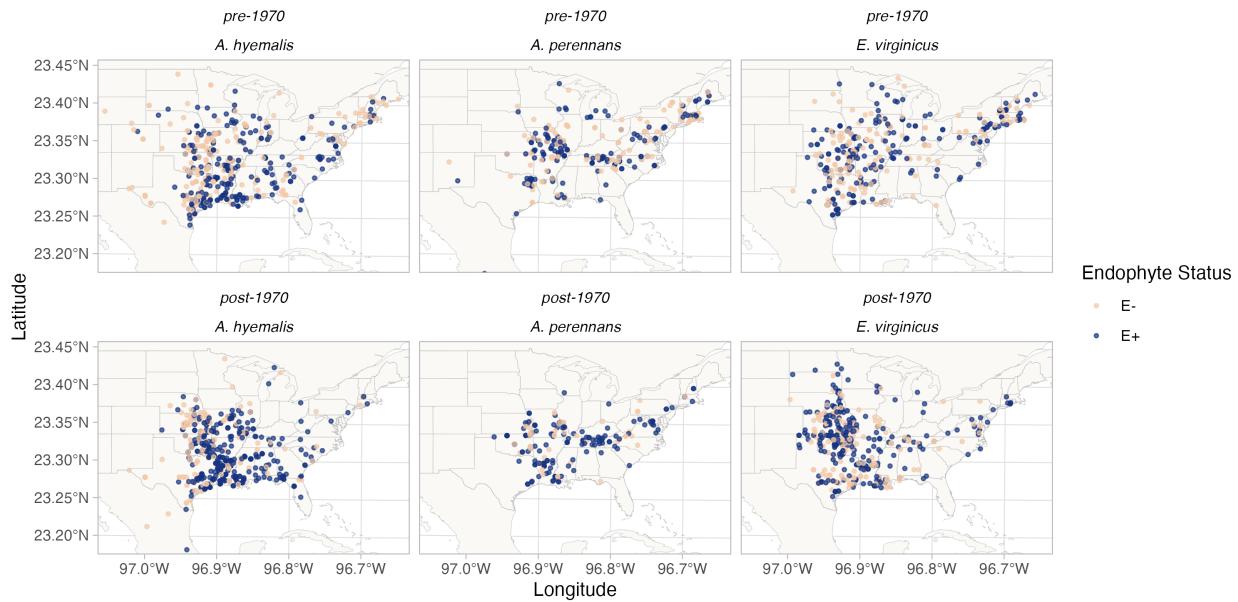


Figure A1: Endophyte presence/absence in specimens of each host species. Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points) and are faceted based on collection period.

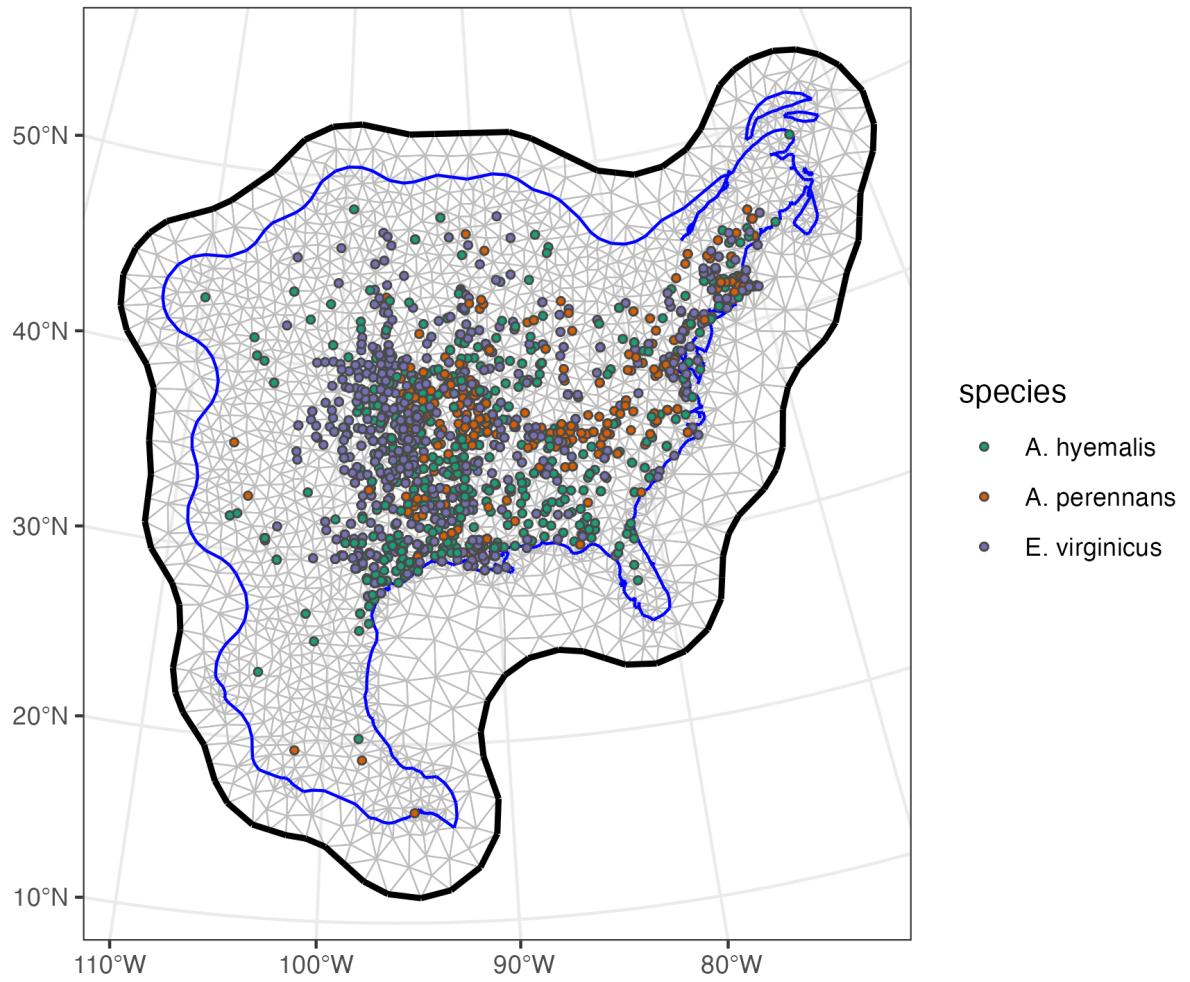


Figure A2: Triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull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

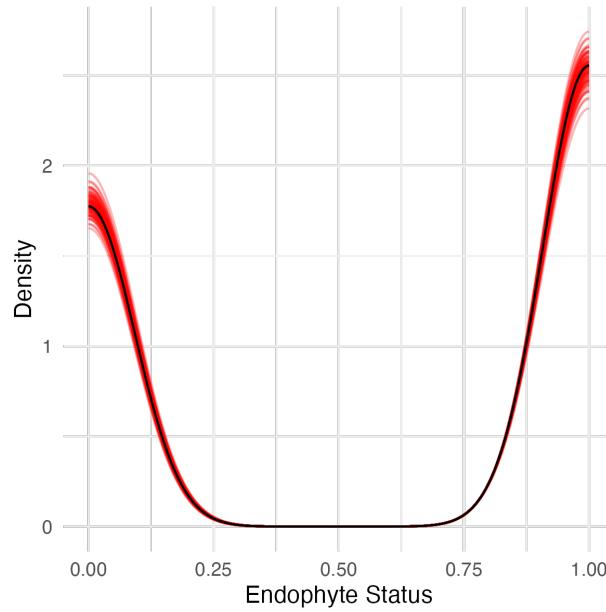


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (black) along with 100 simulated datasets (red).

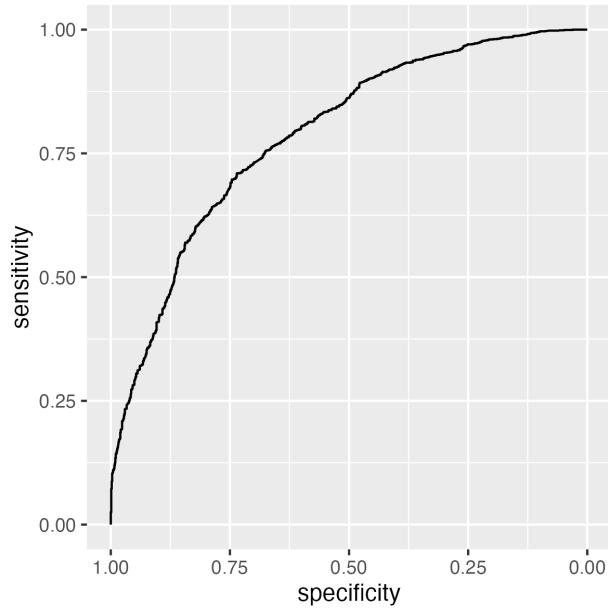


Figure A4: ROC plot showing model performance classifying observations according to endophyte status within the in-sample data. The curves show adequate model performance for observed data. The AUC value is 0.79.

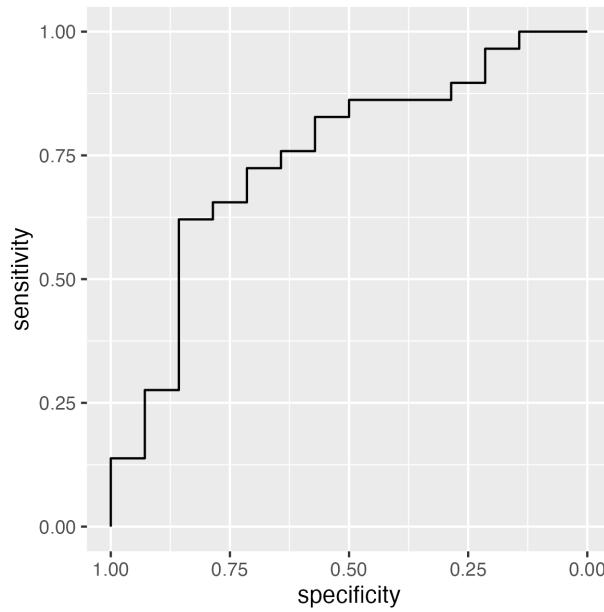


Figure A5: ROC plot showing model performance classifying observations according to endophyte status within the out-of-sample data. The curves show adequate model performance for test data. The AUC value is 0.77.

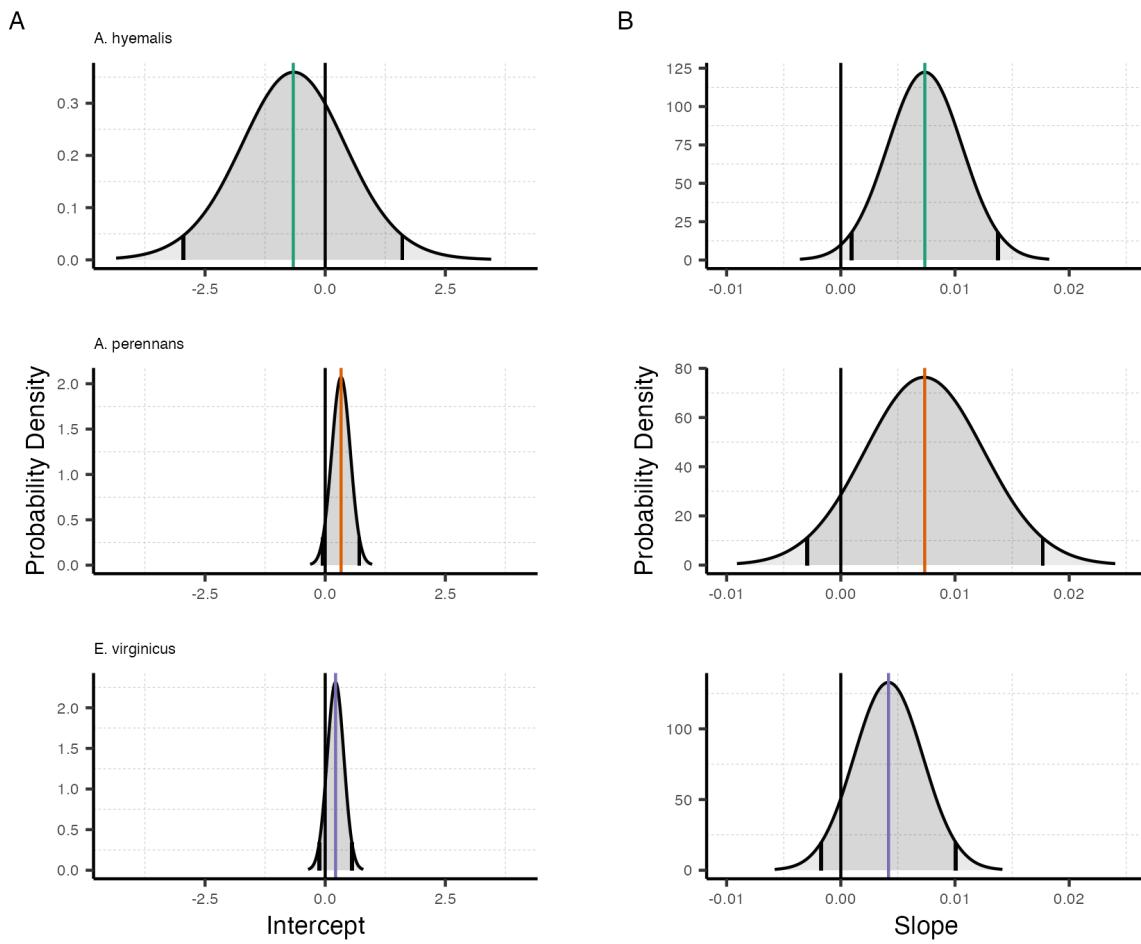


Figure A6: Density curves show the probability density along with mean (colored line) and 95% CI (black lines) for the (A) intercept and (B) slope terms, **A** and **T** respectively. Colors represent each host species

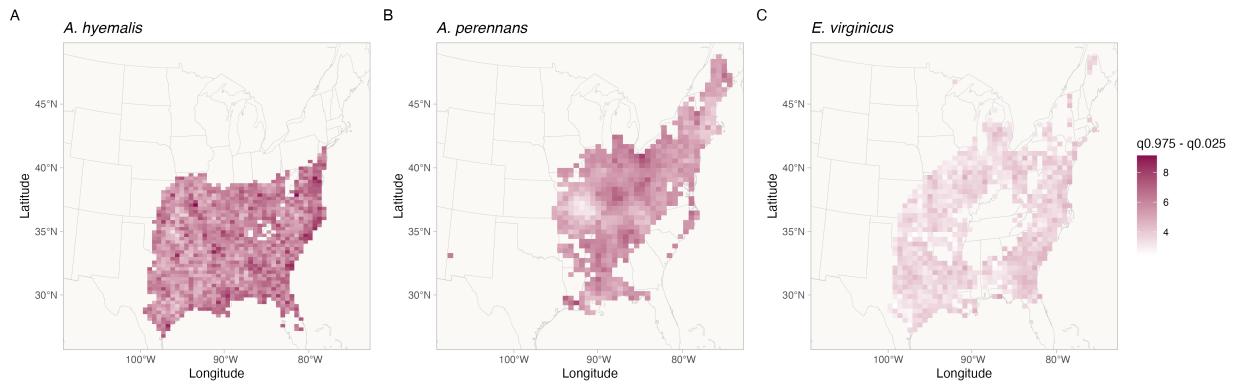


Figure A7: Shading represents the range of the 95% posterior credible interval for spatially varying slopes, τ .

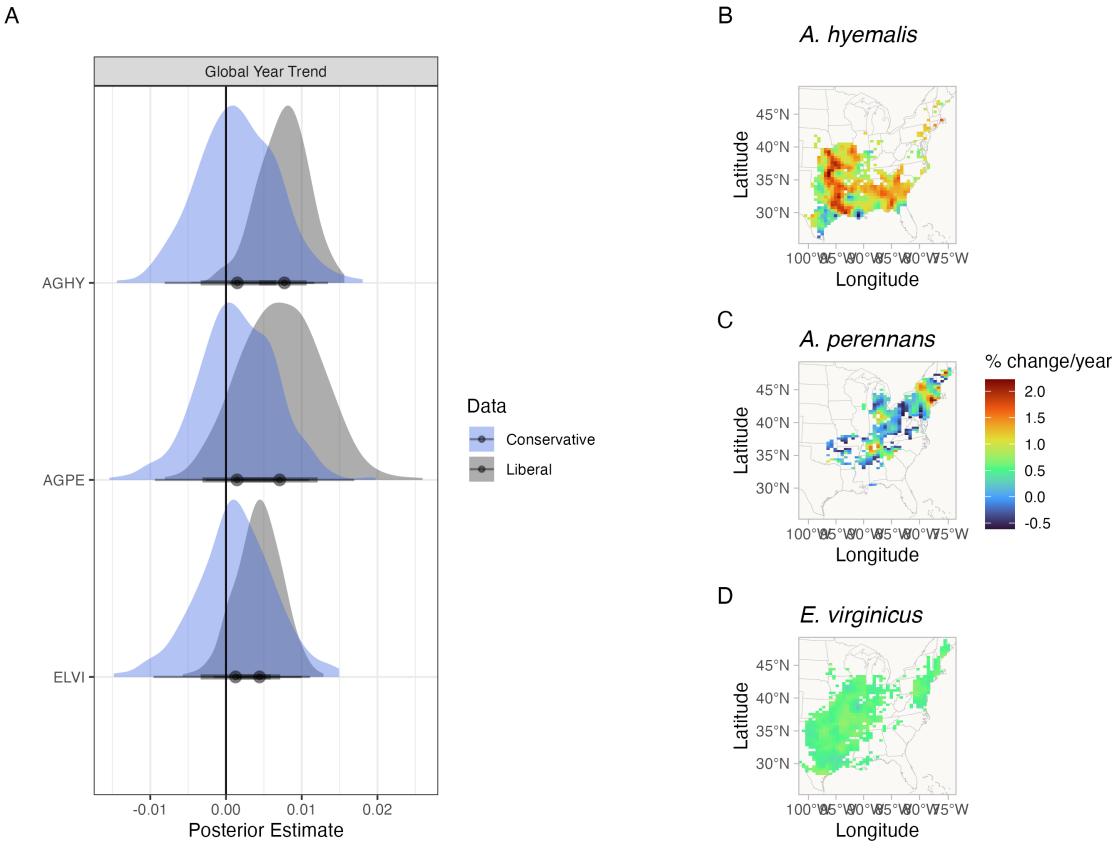


Figure A8: Comparison of liberal versus conservative endophyte scores on modeled outcomes. (A) Posterior estimates of global temporal trend for models fit to liberal scores (grey) and to conservative scores (blue). Maps show the spatially varying temporal trend estimates from model fit to conservative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

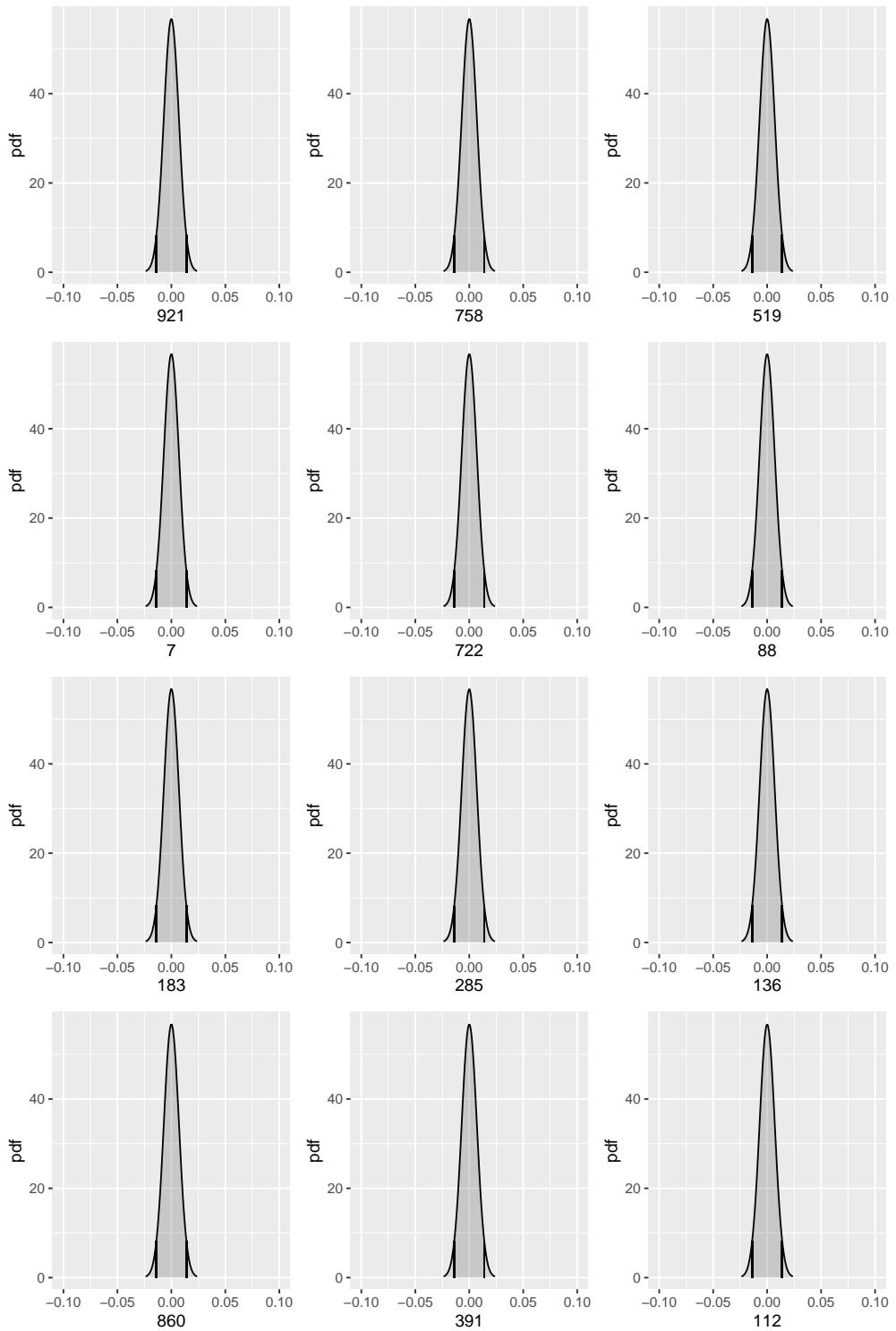


Figure A9: Posterior estimates of collector random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 12 randomly selected collectors.

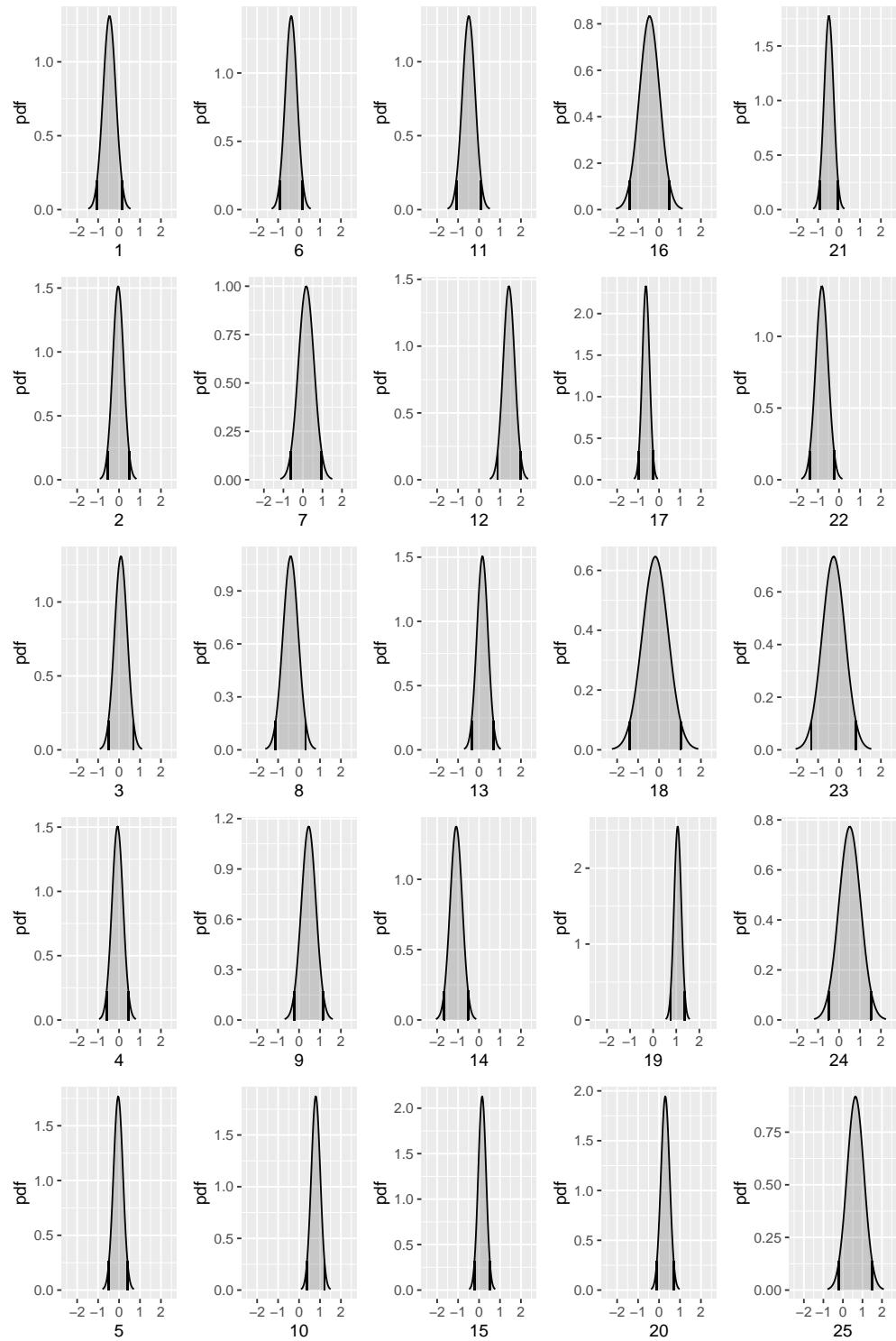


Figure A10: Posterior estimates of scorer random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 25 scorers.

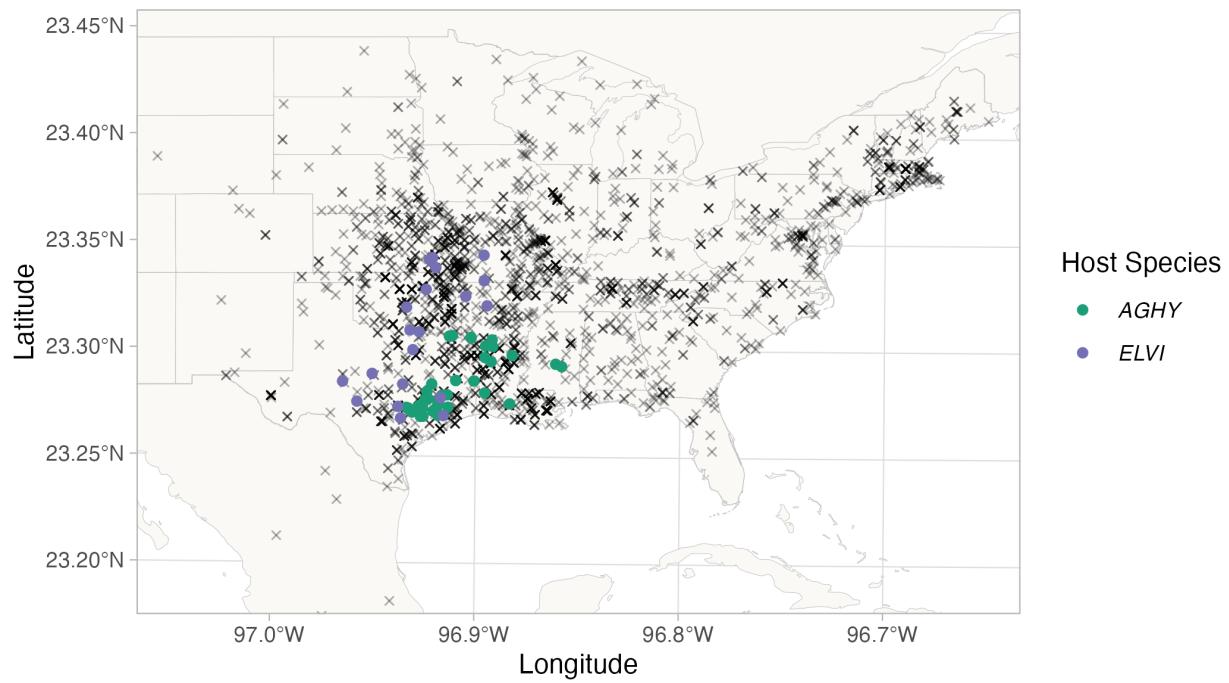


Figure A11: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

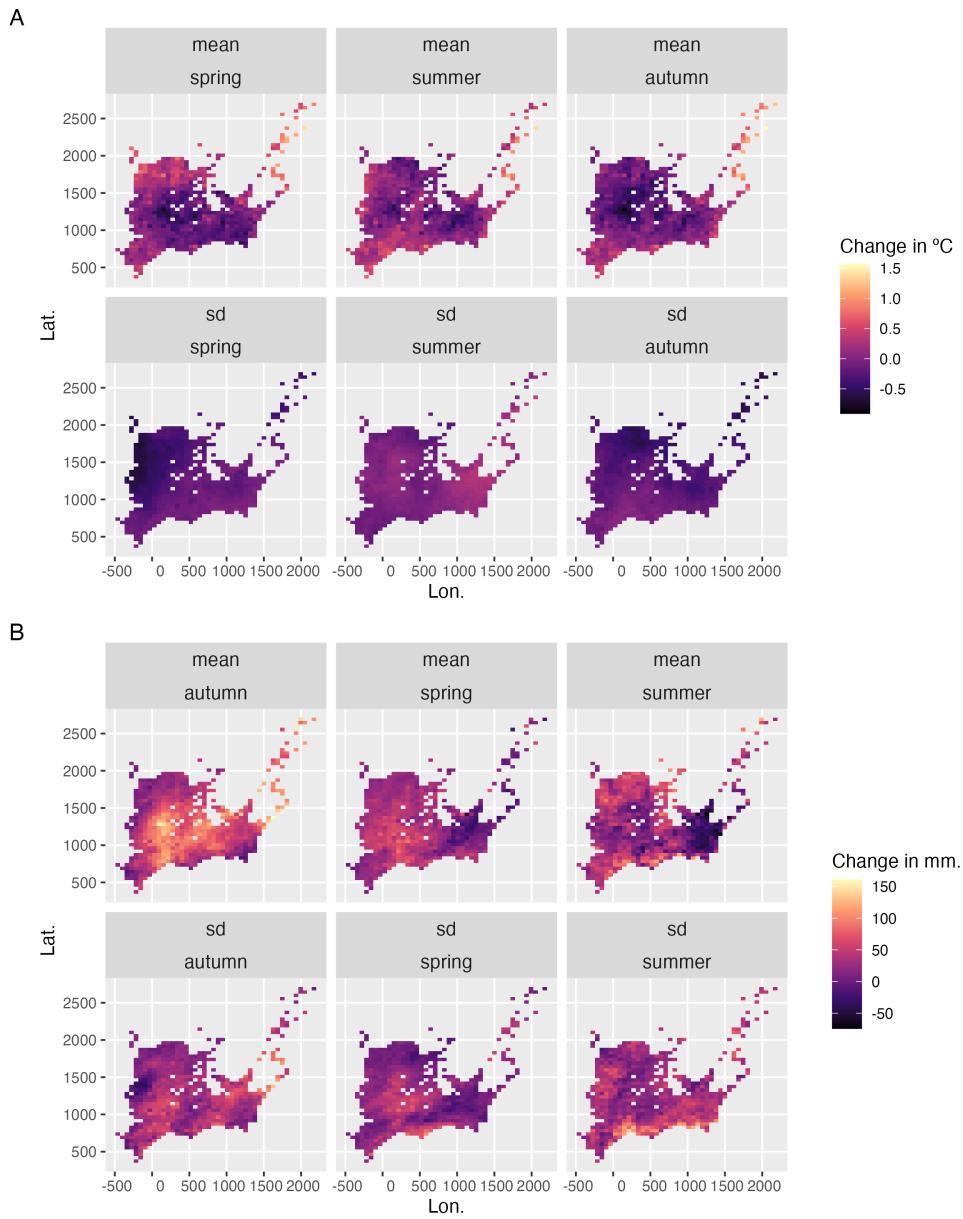


Figure A12: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. hyemalis* used in post-hoc climate correlation analysis.

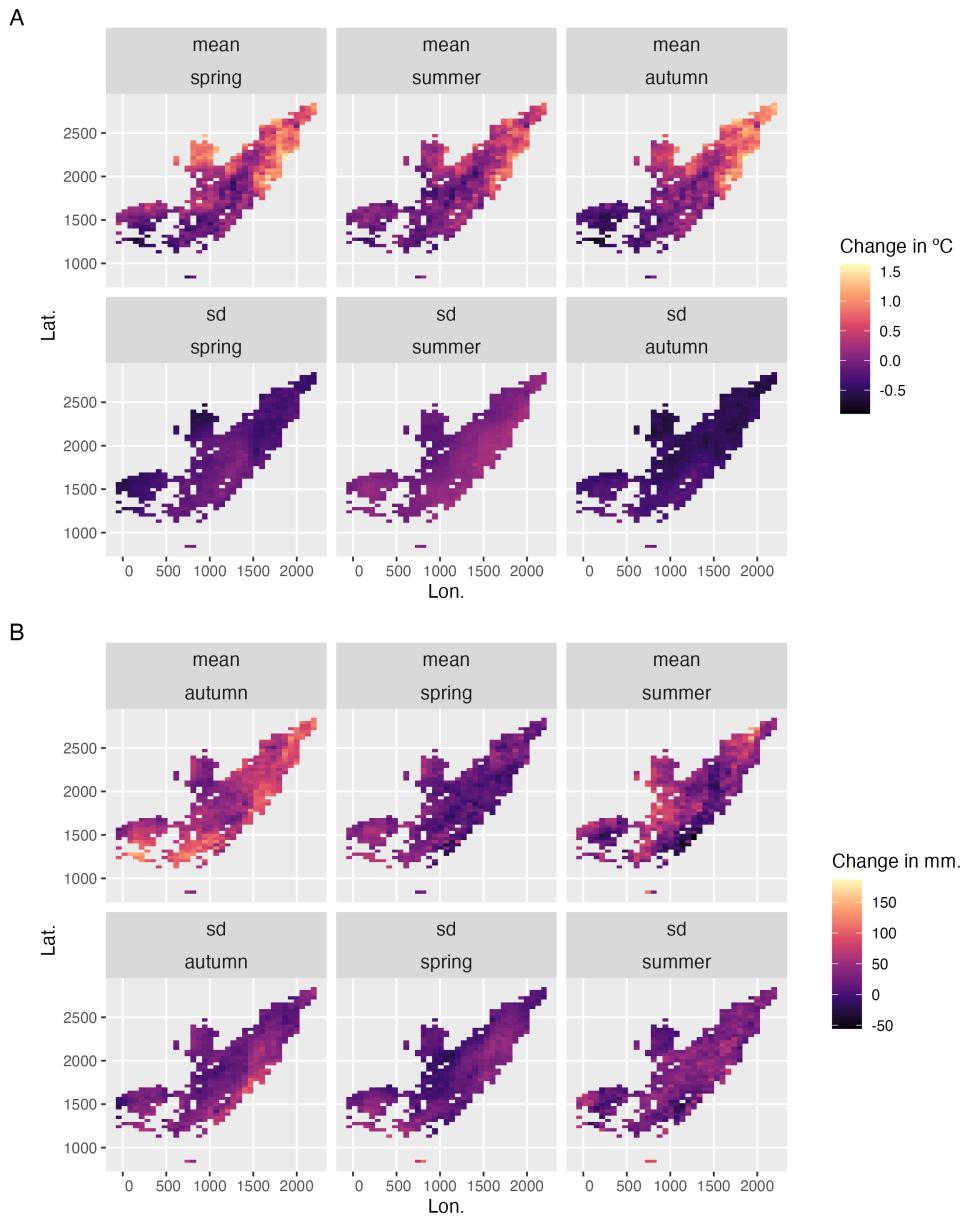


Figure A13: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020.

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.

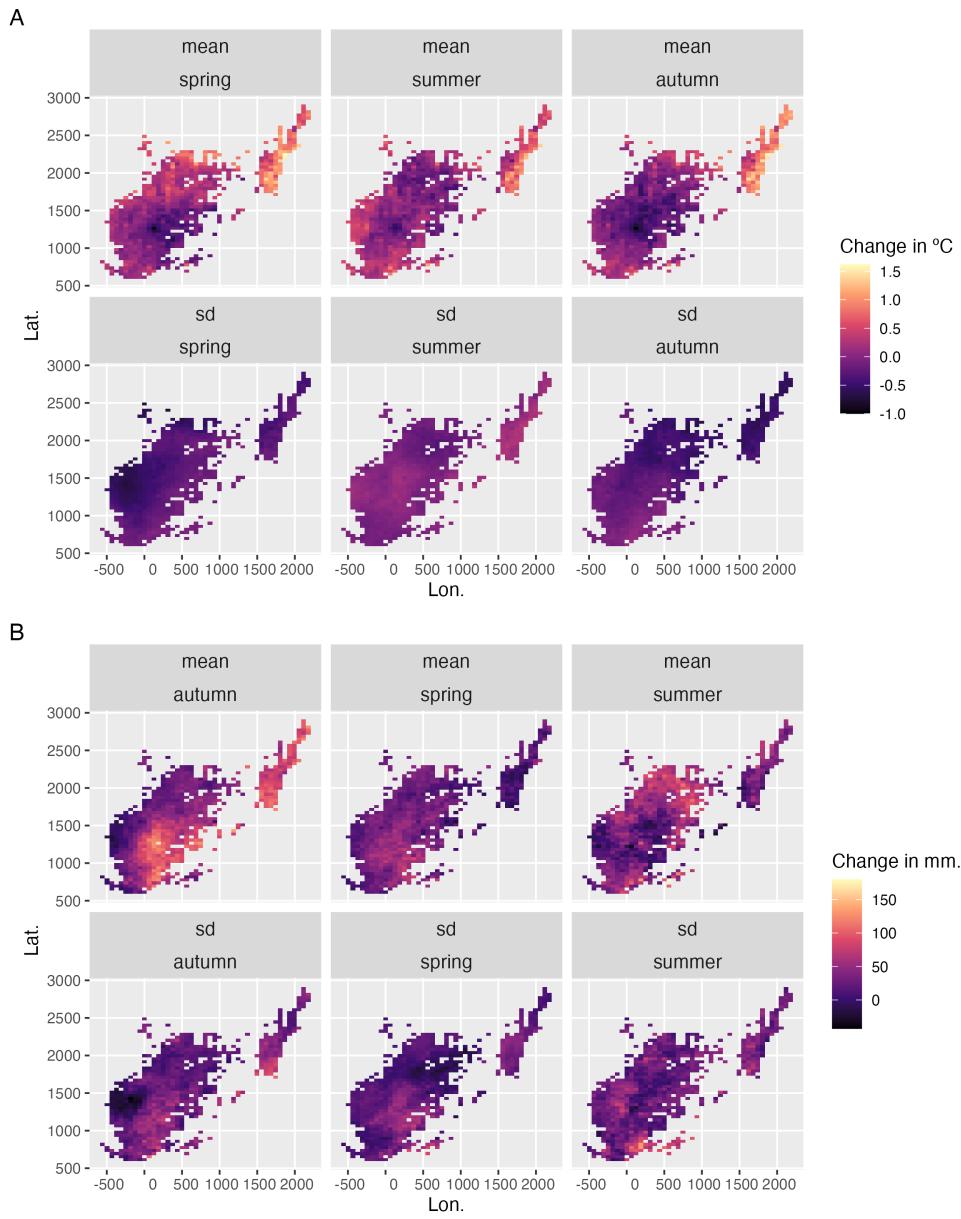


Figure A14: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *E. virginicus* used in post-hoc climate correlation analysis.

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 |

517

Supporting Methods

518

ODMAP Protocol

519 **Overview**

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

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

522 **Study area:** Eastern North America

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

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

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

526 **Boundary:** Natural.

527 **Data**

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

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

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

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

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

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

534 **Model**

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

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

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

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

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

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

543 **Assessment**

544 We used AUC to test model performance.

545 **Prediction**

546 We predicted the probability of presence of the host species as a binary maps (presence or ab-

547 sence)

Literature Cited

- 549 Michelle E Afkhami. Fungal endophyte–grass symbioses are rare in the California floristic
550 province and other regions with mediterranean-influenced climates. *Fungal ecology*, 5(3):345–
551 352, 2012.
- 552 Michelle E Afkhami and Jennifer A Rudgers. Symbiosis lost: imperfect vertical transmission of
553 fungal endophytes in grasses. *The American Naturalist*, 172(3):405–416, 2008.
- 554 Michelle E Afkhami, Patrick J McIntyre, and Sharon Y Strauss. Mutualist-mediated effects on
555 species' range limits across large geographic scales. *Ecology letters*, 17(10):1265–1273, 2014.
- 556 Sally N Aitken, Sam Yeaman, Jason A Holliday, Tongli Wang, and Sierra Curtis-McLane. Adap-
557 tation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary
558 applications*, 1(1):95–111, 2008.
- 559 Clare E Aslan, Erika S Zavaleta, Bernie Tershy, and Donald Croll. Mutualism disruption threatens
560 global plant biodiversity: a systematic review. *PLoS one*, 8(6):e66993, 2013.
- 561 Fabian E Bachl, Finn Lindgren, David L Borchers, and Janine B Illian. inlabru: an R package for
562 bayesian spatial modelling from ecological survey data. *Methods in Ecology and Evolution*, 10(6):
563 760–766, 2019.
- 564 Charles W Bacon and James F White. Stains, media, and procedures for analyzing endophytes.
565 In *Biotechnology of endophytic fungi of grasses*, pages 47–56. CRC Press, 2018.
- 566 Haakon Bakka, Håvard Rue, Geir-Arne Fuglstad, Andrea Riebler, David Bolin, Janine Illian, Elias
567 Krainski, Daniel Simpson, and Finn Lindgren. Spatial modeling with r-inla: A review. *Wiley
568 Interdisciplinary Reviews: Computational Statistics*, 10(6):e1443, 2018.
- 569 Freek T Bakker, Vanessa C Bieker, and Michael D Martin. Herbarium collection-based plant
570 evolutionary genetics and genomics, 2020.

- 571 Dawn R Bazely, John P Ball, Mark Vicari, Andrew J Tanentzap, Myrtille Bérenger, Tomo Rakoc
572 evic, and Saewan Koh. Broad-scale geographic patterns in the distribution of vertically-
573 transmitted, asexual endophytes in four naturally-occurring grasses in sweden. *Ecography*,
574 30(3):367–374, 2007.
- 575 Julien Beguin, Sara Martino, Håvard Rue, and Steven G Cumming. Hierarchical analysis of
576 spatially autocorrelated ecological data using integrated nested laplace approximation. *Methods*
577 in *Ecology and Evolution*, 3(5):921–929, 2012.
- 578 Colette S Berg, Jason L Brown, and Jennifer J Weber. An examination of climate-driven flowering-
579 time shifts at large spatial scales over 153 years in a common weedy annual. *American Journal*
580 of *Botany*, 106(11):1435–1443, 2019.
- 581 Vanessa C Bieker, Fátima Sánchez Barreiro, Jacob A Rasmussen, Marie Brunier, Nathan Wales,
582 and Michael D Martin. Metagenomic analysis of historical herbarium specimens reveals a
583 postmortem microbial community. *Molecular ecology resources*, 20(5):1206–1219, 2020.
- 584 Jessica L Blois, Phoebe L Zarnetske, Matthew C Fitzpatrick, and Seth Finnegan. Climate change
585 and the past, present, and future of biotic interactions. *Science*, 341(6145):499–504, 2013.
- 586 Michael Bradshaw, Uwe Braun, Marianne Elliott, Julia Kruse, Shu-Yan Liu, Guanxiu Guan, and
587 Patrick Tobin. A global genetic analysis of herbarium specimens reveals the invasion dynamics
588 of an introduced plant pathogen. *Fungal Biology*, 125(8):585–595, 2021.
- 589 D Brem and A Leuchtmann. Epichloë grass endophytes increase herbivore resistance in the
590 woodland grass *brachypodium sylvaticum*. *Oecologia*, 126(4):522–530, 2001.
- 591 Tamara A Carleton and Solomon M Hsiang. Social and economic impacts of climate. *Science*, 353
592 (6304):aad9837, 2016.
- 593 Shen Cheng, Ying-Ning Zou, Kamil Kuča, Abeer Hashem, Elsayed Fathi Abd_Allah, and Qiang-

- 594 Sheng Wu. Elucidating the mechanisms underlying enhanced drought tolerance in plants
595 mediated by arbuscular mycorrhizal fungi. *Frontiers in Microbiology*, 12:4029, 2021.
- 596 Keith Clay and Christopher Schardl. Evolutionary origins and ecological consequences of endo-
597 phyte symbiosis with grasses. *the american naturalist*, 160(S4):S99–S127, 2002.
- 598 David G Clayton, Luisa Bernardinelli, and Cristina Montomoli. Spatial correlation in ecological
599 analysis. *International journal of epidemiology*, 22(6):1193–1202, 1993.
- 600 KD Craven, PTW Hsiau, A Leuchtmann, W Hollin, and CL Schardl. Multigene phylogeny of
601 epichloë species, fungal symbionts of grasses. *Annals of the Missouri Botanical Garden*, pages
602 14–34, 2001.
- 603 Kerri M Crawford, John M Land, and Jennifer A Rudgers. Fungal endophytes of native grasses
604 decrease insect herbivore preference and performance. *Oecologia*, 164:431–444, 2010.
- 605 Michael S Crossley, Timothy D Meehan, Matthew D Moran, Jeffrey Glassberg, William E Snyder,
606 and Andrew K Davis. Opposing global change drivers counterbalance trends in breeding north
607 american monarch butterflies. *Global change biology*, 28(15):4726–4735, 2022.
- 608 Christopher Daly and Kirk Bryant. The prism climate and weather system—an introduction.
609 *Corvallis, OR: PRISM climate group*, 2, 2013.
- 610 Barnabas H Daru, Daniel S Park, Richard B Primack, Charles G Willis, David S Barrington,
611 Timothy JS Whitfeld, Tristram G Seidler, Patrick W Sweeney, David R Foster, Aaron M Ellison,
612 et al. Widespread sampling biases in herbaria revealed from large-scale digitization. *New
613 Phytologist*, 217(2):939–955, 2018.
- 614 Barnabas H Daru, Elizabeth A Bowman, Donald H Pfister, and A Elizabeth Arnold. A novel proof
615 of concept for capturing the diversity of endophytic fungi preserved in herbarium specimens.
616 *Philosophical Transactions of the Royal Society B*, 374(1763):20170395, 2019.

- 617 Charles C Davis, Charles G Willis, Bryan Connolly, Courtland Kelly, and Aaron M Ellison.
618 Herbarium records are reliable sources of phenological change driven by climate and pro-
619 vide novel insights into species' phenological cueing mechanisms. *American journal of botany*,
620 102(10):1599–1609, 2015.
- 621 Andrew J Davitt, Marcus Stansberry, and Jennifer A Rudgers. Do the costs and benefits of fungal
622 endophyte symbiosis vary with light availability? *New Phytologist*, 188(3):824–834, 2010.
- 623 Andrew J Davitt, Chris Chen, and Jennifer A Rudgers. Understanding context-dependency in
624 plant–microbe symbiosis: the influence of abiotic and biotic contexts on host fitness and the
625 rate of symbiont transmission. *Environmental and Experimental Botany*, 71(2):137–145, 2011.
- 626 Facundo A Decunta, Luis I Pérez, Dariusz P Malinowski, Marco A Molina-Montenegro, and
627 Pedro E Gundel. A systematic review on the effects of epichloë fungal endophytes on drought
628 tolerance in cool-season grasses. *Frontiers in plant science*, 12:644731, 2021.
- 629 Mauro Di Luzio, Gregory L Johnson, Christopher Daly, Jon K Eischeid, and Jeffrey G Arnold.
630 Constructing retrospective gridded daily precipitation and temperature datasets for the con-
631 terminous united states. *Journal of Applied Meteorology and Climatology*, 47(2):475–497, 2008.
- 632 Marion L Donald, Teresa F Bohner, Kory M Kolis, R Alan Shadow, Jennifer A Rudgers, and
633 Tom EX Miller. Context-dependent variability in the population prevalence and individual
634 fitness effects of plant–fungal symbiosis. *Journal of Ecology*, 109(2):847–859, 2021.
- 635 AE Douglas. Host benefit and the evolution of specialization in symbiosis. *Heredity*, 81(6):599–
636 603, 1998.
- 637 Yuan-Wen Duan, Haibao Ren, Tao Li, Lin-Lin Wang, Zhi-Qiang Zhang, Yan-Li Tu, and Yong-Ping
638 Yang. A century of pollination success revealed by herbarium specimens of seed pods. *New
639 Phytologist*, 224(4):1512–1517, 2019.

- 640 Erika J Edwards, Brent D Mishler, and Charles D Davis. University herbaria are uniquely impor-
641 tant. *Trends in Plant Science*.
- 642 Markus Engel, Tobias Mette, and Wolfgang Falk. Spatial species distribution models: Using
643 bayes inference with inla and spde to improve the tree species choice for important european
644 tree species. *Forest Ecology and Management*, 507:119983, 2022.
- 645 Sanne M Evers, Tiffany M Knight, David W Inouye, Tom EX Miller, Roberto Salguero-Gómez,
646 Amy M Iler, and Aldo Compagnoni. Lagged and dormant season climate better predict plant
647 vital rates than climate during the growing season. *Global Change Biology*, 27(9):1927–1941,
648 2021.
- 649 Paul EM Fine. Vectors and vertical transmission: an epidemiologic perspective. *Annals of the New
650 York Academy of Sciences*, 266(1):173–194, 1975.
- 651 Joshua C Fowler, Shaun Ziegler, Kenneth D Whitney, Jennifer A Rudgers, and Tom EX Miller.
652 Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity.
653 *Ecology Letters*, 27(5):e14438, 2024.
- 654 PR Fraude, F De Jongh, F Vermeulen, J Van Bleijswijk, and RPM Bak. Variation in symbiont
655 distribution between closely related coral species over large depth ranges. *Molecular Ecology*,
656 17(2):691–703, 2008.
- 657 Sarah E Gilman, Mark C Urban, Joshua Tewksbury, George W Gilchrist, and Robert D Holt. A
658 framework for community interactions under climate change. *Trends in ecology & evolution*, 25
659 (6):325–331, 2010.
- 660 Gustaf Granath, Mark Vicari, Dawn R Bazely, John P Ball, Adriana Puentes, and Tomo Rakoce-
661 vic. Variation in the abundance of fungal endophytes in fescue grasses along altitudinal and
662 grazing gradients. *Ecography*, 30(3):422–430, 2007.
- 663 Andrin Gross, Célia Petitcollin, Cyril Dutech, Bayo Ly, Marie Massot, Julie Faivre d'Arcier, Laure

- 664 Dubois, Gilles Saint-Jean, and Marie-Laure Desprez-Loustau. Hidden invasion and niche con-
665 traction revealed by herbaria specimens in the fungal complex causing oak powdery mildew
666 in europe. *Biological Invasions*, 23:885–901, 2021.
- 667 Edmund M. Hart and Kendon Bell. prism: Download data from the oregon prism project. 2015.
668 doi: 10.5281/zenodo.33663. URL <https://github.com/ropensci/prism>. R package version
669 0.0.6.
- 670 J Mason Heberling and David J Burke. Utilizing herbarium specimens to quantify historical
671 mycorrhizal communities. *Applications in plant sciences*, 7(4):e01223, 2019.
- 672 Robert J Hijmans, Steven Phillips, John Leathwick, Jane Elith, and Maintainer Robert J Hijmans.
673 Package ‘dismo’. *Circles*, 9(1):1–68, 2017.
- 674 Janneke HilleRisLambers, Melanie A Harsch, Ailene K Ettinger, Kevin R Ford, and Elinore J
675 Theobald. How will biotic interactions influence climate change-induced range shifts? *Annals*
676 *of the New York Academy of Sciences*, 1297(1):112–125, 2013.
- 677 IPCC. Climate change 2021: The physical science basis, 2021. URL
678 <https://www.ipcc.ch/report/ar6/wg1/>.
- 679 Nick JB Isaac, Marta A Jarzyna, Petr Keil, Lea I Dambly, Philipp H Boersch-Supan, Ella Browning,
680 Stephen N Freeman, Nick Golding, Gurutzeta Guillera-Arroita, Peter A Henrys, et al. Data
681 integration for large-scale models of species distributions. *Trends in ecology & evolution*, 35(1):
682 56–67, 2020.
- 683 Alberto Jiménez-Valverde. Insights into the area under the receiver operating characteristic curve
684 (auc) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeog-*
685 *rphy*, 21(4):498–507, 2012.
- 686 David Kahle, Hadley Wickham, and Maintainer David Kahle. Package ‘ggmap’. *Retrieved Septem-*
687 *ber*, 5:2021, 2019.

- 688 Melanie R Kazenel, Catherine L Debban, Luciana Ranelli, Will Q Hendricks, Y Anny Chung,
689 Thomas H Pendergast IV, Nikki D Charlton, Carolyn A Young, and Jennifer A Rudgers. A
690 mutualistic endophyte alters the niche dimensions of its host plant. *AoB plants*, 7:plv005, 2015.
- 691 Roland A Knapp, Gary M Fellers, Patrick M Kleeman, David AW Miller, Vance T Vredenburg,
692 Erica Bree Rosenblum, and Cheryl J Briggs. Large-scale recovery of an endangered amphibian
693 despite ongoing exposure to multiple stressors. *Proceedings of the National Academy of Sciences*,
694 113(42):11889–11894, 2016.
- 695 Mikhail V Kozlov, Irina V Sokolova, Vitali Zverev, Alexander A Egorov, Mikhail Y Goncharov,
696 and Elena L Zvereva. Biases in estimation of insect herbivory from herbarium specimens.
697 *Scientific Reports*, 10(1):12298, 2020.
- 698 Benjamin R Lee, Evelyn F Alecrim, Tara K Miller, Jessica RK Forrest, J Mason Heberling,
699 Richard B Primack, and Risa D Sargent. Phenological mismatch between trees and wildflow-
700 ers: Reconciling divergent findings in two recent analyses. *Journal of Ecology*, 112(6):1184–1199,
701 2024.
- 702 James Lendemer, Barbara Thiers, Anna K Monfils, Jennifer Zaspel, Elizabeth R Ellwood, Andrew
703 Bentley, Katherine LeVan, John Bates, David Jennings, Dori Contreras, et al. The extended
704 specimen network: A strategy to enhance us biodiversity collections, promote research and
705 education. *BioScience*, 70(1):23–30, 2020.
- 706 A Leuchtmann. Systematics, distribution, and host specificity of grass endophytes. *Natural Toxins*,
707 1(3):150–162, 1992.
- 708 Adrian Leuchtmann, Charles W Bacon, Christopher L Schardl, James F White Jr, and Mariusz
709 Tadych. Nomenclatural realignment of neotyphodium species with genus epichloë. *Mycologia*,
710 106(2):202–215, 2014.
- 711 Finn Lindgren, Håvard Rue, and Johan Lindström. An explicit link between gaussian fields and

- 712 gaussian markov random fields: the stochastic partial differential equation approach. *Journal*
713 *of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4):423–498, 2011.
- 714 Canran Liu, Pam M Berry, Terence P Dawson, and Richard G Pearson. Selecting thresholds of
715 occurrence in the prediction of species distributions. *Ecography*, 28(3):385–393, 2005.
- 716 Margaret McFall-Ngai, Michael G Hadfield, Thomas CG Bosch, Hannah V Carey, Tomislav
717 Domazet-Lošo, Angela E Douglas, Nicole Dubilier, Gerard Eberl, Tadashi Fukami, Scott F
718 Gilbert, et al. Animals in a bacterial world, a new imperative for the life sciences. *Proceedings*
719 *of the National Academy of Sciences*, 110(9):3229–3236, 2013.
- 720 Timothy D Meehan, Nicole L Michel, and Håvard Rue. Spatial modeling of audubon christmas
721 bird counts reveals fine-scale patterns and drivers of relative abundance trends. *Ecosphere*, 10
722 (4):e02707, 2019.
- 723 Emily K Meineke, Charles C Davis, and T Jonathan Davies. The unrealized potential of herbaria
724 for global change biology. *Ecological Monographs*, 88(4):505–525, 2018.
- 725 Emily K Meineke, Aimée T Classen, Nathan J Sanders, and T Jonathan Davies. Herbarium
726 specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1):105–117,
727 2019.
- 728 Abigail R Meyer, Maria Valentin, Laima Liulevicius, Tami R McDonald, Matthew P Nelsen, Jean
729 Pengra, Robert J Smith, and Daniel Stanton. Climate warming causes photobiont degradation
730 and c starvation in a boreal climate sentinel lichen. *American Journal of Botany*, 2022.
- 731 David AW Miller, Krishna Pacifici, Jamie S Sanderlin, and Brian J Reich. The recent past and
732 promising future for data integration methods to estimate species' distributions. *Methods in*
733 *Ecology and Evolution*, 10(1):22–37, 2019.
- 734 Daniel S Park, Ian Breckheimer, Alex C Williams, Edith Law, Aaron M Ellison, and Charles C
735 Davis. Herbarium specimens reveal substantial and unexpected variation in phenological sen-

- 736 sitivity across the eastern united states. *Philosophical Transactions of the Royal Society B*, 374
737 (1763):20170394, 2019.
- 738 Martin Parniske. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Reviews
739 Microbiology*, 6(10):763–775, 2008.
- 740 Anton Pauw and Julie A Hawkins. Reconstruction of historical pollination rates reveals linked
741 declines of pollinators and plants. *Oikos*, 120(3):344–349, 2011.
- 742 Shilong Piao, Qiang Liu, Anping Chen, Ivan A Janssens, Yongshuo Fu, Junhu Dai, Lingli Liu,
743 XU Lian, Miaogen Shen, and Xiaolin Zhu. Plant phenology and global climate change: Current
744 progresses and challenges. *Global change biology*, 25(6):1922–1940, 2019.
- 745 Timothée Poisot, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew Mac-
746 Donald, Benjamin Mercier, Clément Violet, and Steve Vissault. Global knowledge gaps in
747 species interaction networks data. *Journal of Biogeography*, 48(7):1552–1563, 2021.
- 748 Nicole E Rafferty, Paul J CaraDonna, and Judith L Bronstein. Phenological shifts and the fate of
749 mutualisms. *Oikos*, 124(1):14–21, 2015.
- 750 Christopher J Raxworthy and Brian Tilston Smith. Mining museums for historical dna: advances
751 and challenges in museomics. *Trends in Ecology & Evolution*, 36(11):1049–1060, 2021.
- 752 François Renoz, Inès Pons, and Thierry Hance. Evolutionary responses of mutualistic insect-
753 bacterial symbioses in a world of fluctuating temperatures. *Current opinion in insect science*, 35:
754 20–26, 2019.
- 755 Elizabeth Lewis Roberts and Aileen Ferraro. Rhizosphere microbiome selection by epichloë en-
756 dophytes of festuca arundinacea. *Plant and soil*, 396:229–239, 2015.
- 757 RJ Rodriguez, JF White Jr, Anne E Arnold, and a RS and Redman. Fungal endophytes: diversity
758 and functional roles. *New phytologist*, 182(2):314–330, 2009.

- 759 Gregor Rolshausen, Francesco Dal Grande, Anna D Sadowska-Deś, Jürgen Otte, and Imke
760 Schmitt. Quantifying the climatic niche of symbiont partners in a lichen symbiosis indicates
761 mutualist-mediated niche expansions. *Ecography*, 41(8):1380–1392, 2018.
- 762 Jennifer A Rudgers and Angela L Swafford. Benefits of a fungal endophyte in *elymus virginicus*
763 decline under drought stress. *Basic and Applied Ecology*, 10(1):43–51, 2009.
- 764 Jennifer A Rudgers, Michelle E Afkhami, Megan A Rúa, Andrew J Davitt, Samantha Hammer,
765 and Valérie M Huguet. A fungus among us: broad patterns of endophyte distribution in the
766 grasses. *Ecology*, 90(6):1531–1539, 2009.
- 767 Jennifer A Rudgers, Rebecca A Fletcher, Eric Olivas, Carolyn A Young, Nikki D Charlton, Dean E
768 Pearson, and John L Maron. Long-term ungulate exclusion reduces fungal symbiont prevalence
769 in native grasslands. *Oecologia*, 181:1151–1161, 2016.
- 770 Håvard Rue, Sara Martino, and Nicolas Chopin. Approximate bayesian inference for latent gaus-
771 sian models by using integrated nested laplace approximations. *Journal of the royal statistical
772 society: Series b (statistical methodology)*, 71(2):319–392, 2009.
- 773 Kari Saikkonen, Pedro E Gundel, and Marjo Helander. Chemical ecology mediated by fungal
774 endophytes in grasses. *Journal of chemical ecology*, 39:962–968, 2013.
- 775 Michelle E Sneck, Jennifer A Rudgers, Carolyn A Young, and Tom EX Miller. Variation in the
776 prevalence and transmission of heritable symbionts across host populations in heterogeneous
777 environments. *Microbial Ecology*, 74:640–653, 2017.
- 778 Thomas F Stocker, Dahe Qin, G-K Plattner, Lisa V Alexander, Simon K Allen, Nathaniel L Bindoff,
779 F-M Bréon, John A Church, Ulrich Cubasch, Seita Emori, et al. Technical summary. In *Climate
780 change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment
781 Report of the Intergovernmental Panel on Climate Change*, pages 33–115. Cambridge University
782 Press, 2013.

- 783 Peter A Stott, Nathan P Gillett, Gabriele C Hegerl, David J Karoly, Dáithí A Stone, Xuebin Zhang,
784 and Francis Zwiers. Detection and attribution of climate change: a regional perspective. *Wiley*
785 *interdisciplinary reviews: climate change*, 1(2):192–211, 2010.
- 786 S Sully, DE Burkepile, MK Donovan, G Hodgson, and R Van Woesik. A global analysis of coral
787 bleaching over the past two decades. *Nature communications*, 10(1):1–5, 2019.
- 788 E Toby Kiers, Todd M Palmer, Anthony R Ives, John F Bruno, and Judith L Bronstein. Mutualisms
789 in a changing world: an evolutionary perspective. *Ecology letters*, 13(12):1459–1474, 2010.
- 790 Andrew T Tredennick, Giles Hooker, Stephen P Ellner, and Peter B Adler. A practical guide to
791 selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102(6):e03336,
792 2021.
- 793 Amy M Truitt, Martin Kapun, Rupinder Kaur, and Wolfgang J Miller. Wolbachia modifies thermal
794 preference in *drosophila melanogaster*. *Environmental microbiology*, 21(9):3259–3268, 2019.
- 795 Shripad D. Tuljapurkar. Population dynamics in variable environments. III. Evo-
796 lutionary dynamics of r-selection. *Theoretical Population Biology*, 21(1):141–165,
797 February 1982. ISSN 0040-5809. doi: 10.1016/0040-5809(82)90010-7. URL
798 <http://www.sciencedirect.com/science/article/pii/0040580982900107>.
- 799 Arantxa Urdangarin, Tomás Goicoa, and María Dolores Ugarte. Evaluating recent methods to
800 overcome spatial confounding. *Revista Matemática Complutense*, 36(2):333–360, 2023.
- 801 Veronika Vikuk, Carolyn A Young, Stephen T Lee, Padmaja Nagabhyru, Markus Krischke, Mar-
802 tin J Mueller, and Jochen Krauss. Infection rates and alkaloid patterns of different grass species
803 with systemic epichloë endophytes. *Applied and Environmental Microbiology*, 85(17):e00465–19,
804 2019.
- 805 Zhengfeng Wang, Chunjie Li, and James White. Effects of epichloë endophyte infection on

- 806 growth, physiological properties and seed germination of wild barley under saline conditions.
807 *Journal of Agronomy and Crop Science*, 206(1):43–51, 2020.
- 808 Robert J Warren and Mark A Bradford. Mutualism fails when climate response differs between
809 interacting species. *Global Change Biology*, 20(2):466–474, 2014.
- 810 Nicole S Webster, Rose E Cobb, and Andrew P Negri. Temperature thresholds for bacterial
811 symbiosis with a sponge. *The ISME journal*, 2(8):830–842, 2008.
- 812 James F White and Garry T Cole. Endophyte-host associations in forage grasses. i. distribution
813 of fungal endophytes in some species of lolium and festuca. *Mycologia*, 77(2):323–327, 1985.
- 814 Franziska M Willems, JF Scheepens, and Oliver Bossdorf. Forest wildflowers bloom earlier as
815 europe warms: lessons from herbaria and spatial modelling. *New Phytologist*, 235(1):52–65,
816 2022.
- 817 Charles G Willis, Elizabeth R Ellwood, Richard B Primack, Charles C Davis, Katelin D Pearson,
818 Amanda S Gallinat, Jenn M Yost, Gil Nelson, Susan J Mazer, Natalie L Rossington, et al. Old
819 plants, new tricks: Phenological research using herbarium specimens. *Trends in ecology &*
820 *evolution*, 32(7):531–546, 2017.
- 821 Chao Xia, Nana Li, Yawen Zhang, Chunjie Li, Xingxu Zhang, and Zhibiao Nan. Role of epichloë
822 endophytes in defense responses of cool-season grasses to pathogens: A review. *Plant disease*,
823 102(11):2061–2073, 2018.
- 824 Kentaro Yoshida, Eriko Sasaki, and Sophien Kamoun. Computational analyses of ancient
825 pathogen dna from herbarium samples: challenges and prospects. *Frontiers in plant science*,
826 6:771, 2015.