

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; ¹1. University of Miami,
⁵ Department of Biology, Miami, Florida;
⁶ * Corresponding author; e-mail: jcf221@miami.edu.

⁷ *Manuscript elements:* Figure 1, figure 2, table 1, appendix A (for print; including figure A1,
⁸ figure A2, and table A1), supplemental PDF. Figure 2 is to print in color.

⁹ *Keywords:* .

¹⁰ *Manuscript type:* Article.

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

¹ *I think this is should be 2*

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 drivers**² corresponding to each host species' peak growing season. 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.³

²*Describe "changes" – warming? drying?*

³*I 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

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

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

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

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

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

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

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

97 Early research on *Epichloë* used herbarium specimens to describe the broad taxonomic di-
98 versity of host species that harbor these symbionts (White and Cole, 1985), establishing that
99 endophyte symbiosis could be identified in plant tissue from as early as 1851.⁴ However, no
100 subsequent studies, to our knowledge, have used the vast resources of biological collections to
101 quantitatively assess spatio-temporal trends in endophyte prevalence and their environmental
102 correlates. Biological collections have been used to demonstrate ecological signatures of climate
103 change, however the predictive ability of these historical analyses is rarely tested. Grasses are
104 commonly collected and identified based on the presence of their reproductive structures, mean-
105 ing that preserved specimens typically contain seeds, conveniently preserving the fungi along
106 with their host plants on herbarium sheets. This creates the opportunity to leverage the unique
107 spatio-temporal sampling of herbarium collections to examine the response of the symbiosis to
108 historical climate change.

109 In this study, we assessed the long-term responses of endophyte symbiosis to climate change

⁴Edited this a bit. This is the earliest year we have in the database that was part of JFWhites original paper.

110 through the use of herbarium specimens of three North American host grass species (*Agrostis*
111 *hyemalis*, *Agrostis perennans*, and *Elymus virginicus*). We first address questions describing spatial
112 and temporal trends in endophyte prevalence: (i) How has endophyte prevalence changed over
113 the past two centuries? and (ii) How spatially heterogenous are temporal trends in endophyte
114 prevalence across eastern North America? We then address how climate change may be driving
115 trends in endophyte prevalence by asking: (iii) What is the relationship between variation in
116 temporal trends in endophyte prevalence and changes in climate drivers? We predicted that
117 aggregate endophyte prevalence would increase over time in tandem with climate warming, and
118 that hotspots of endophyte change would correspond spatially to hotspots of climate change.
119 Finally, we evaluated the performance models built on data from historic specimens with an out-
120 of-sample test, data on endophyte prevalence from contemporary surveys of host populations.
121 To answer these questions we examined a total of 2,346 specimens collected across eastern North
122 America between 1824 and 2019. ⁵

123 Methods

124 Focal species

125 Our surveys focused on three native North American grasses: *Agrostis hyemalis*, *Agrostis peren-*
126 *nans*, and *Elymus virginicus*. Both *Agrostis* species host *Epichloë amarillans* (Craven et al., 2001;
127 Leuchtmann et al., 2014), while *Elymus virginicus* typically hosts *Epichloë elymi* (Clay and Schardl,
128 2002). These C₃ grass species are commonly represented in natural history collections with broad
129 distributions covering much the eastern United States. *A. hyemalis* is a small short-lived perennial
130 species that germinates in the spring and typically flowers between March and July (most com-
131 mon collection month: May). *A. perennans* is of similar stature but is longer lived than *Agrostis*
132 *hyemalis* and flowers in late summer and early autumn (most common collection month: Septem-

⁵I 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.

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

140 *Herbarium surveys*

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

158 After collecting seed samples, we quantified the presence or absence of *Epichloë* fungal hy-

159 phae, which grow intercellularly, in each specimen using microscopy. We first softened seeds
160 with a 10% NaOH solution, then stained the seeds with aniline blue-lactic acid stain and squashed
161 them under a microscope cover slip. We examined the squashed seeds for the presence of fungal
162 hyphae at 200-400X magnification (Bacon and White, 2018). In some cases, the tissues examined
163 during microscopy came from flowers or otherwise non-viable seeds, which were excluded for
164 that specimen. On average we scored 4.7 seeds per specimen of *A. hyemalis*, 4.2 seeds per spec-
165 imen of *A. perennans*, and 3.8 seeds per specimen of *E. virginicus*; we scored # seeds in total. . .
166 Due to imperfect vertical transmission (Afkhami and Rudgers, 2008), it is possible that symbiotic
167 host-plants produce a mixture of symbiotic and non-symbiotic seeds. We therefore designated a
168 specimen as endophyte-symbiotic if *Epichloë* hyphae were observed in one or more of its seeds,
169 or non-symbiotic if hyphae were observed in none of its seeds. To capture uncertainty in the
170 endophyte scoring process, we recorded both a "liberal" and a "conservative" endophyte status
171 for each plant specimen. When we identified potential endophytes with unusual morphology,
172 low uptake of stain, or a small amount of fungal hyphae across the scored seeds, we recorded a
173 positive liberal status (more likely to be endophyte-positive) and a negative conservative status
174 (less likely to be endophyte-positive). 89% of scored plants had matching liberal and conservative
175 scores, reflecting high confidence in endophyte status. The following analyses in the main text
176 used the liberal status, but we repeated all analyses with the conservative status which yielded
177 qualitatively similar results (Fig. A10)

178 *Modeling spatial and temporal changes in endophyte prevalence*

179 We assessed spatial and temporal changes in endophyte prevalence across each host distribu-
180 tion, first quantifying the "global" trends, aggregating across space, and then examining spatial
181 heterogeneity in the direction and magnitude of endophyte change (hotspots and coldspots)
182 across the spatial extent of each host's distribution. To appropriately account for the spatial
183 non-independence of geo-referenced occurrences, we used an approximate Bayesian method,
184 Integrated Nested Laplace Approximation (INLA), to construct spatio-temporal models of endo-

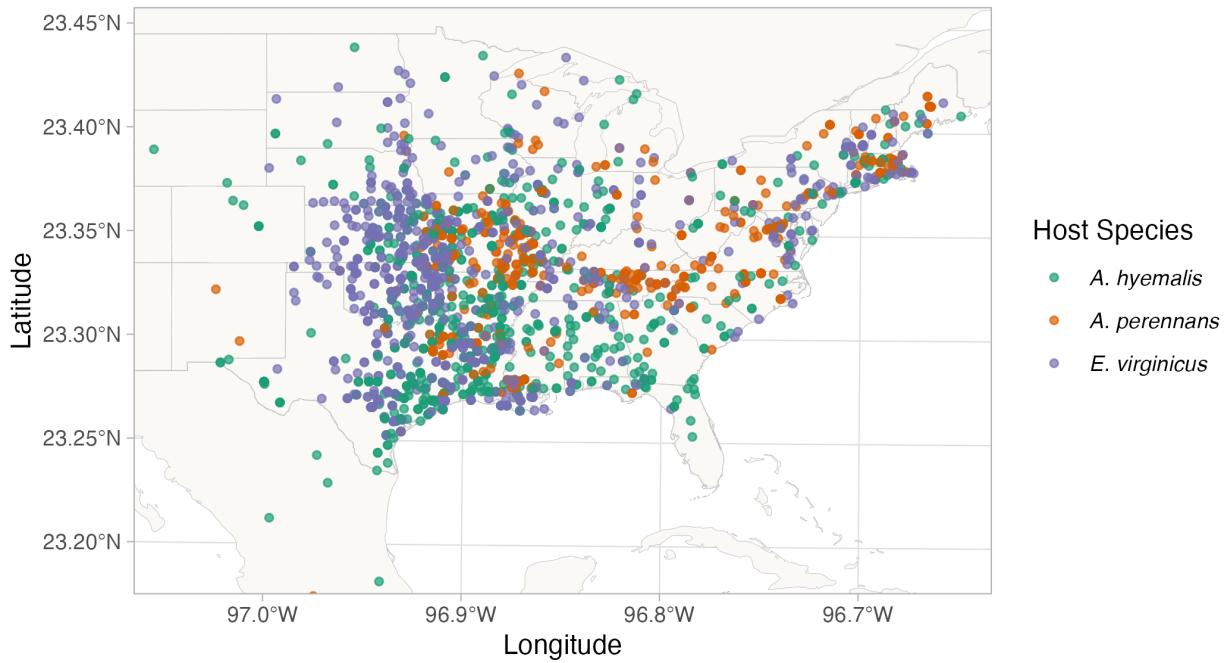


Figure 1: Collection locations of herbarium specimens of three grass host species across eastern North America that were sampled for *Epichloë* endophyte presence or absence.

phyte 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). Fitting models with structured spatial effects is possible with MCMC sampling but can require long computation times, making INLA an effective alternative, which has been used to model spatial patterns in flowering phenology (Willems et al., 2022), the abundance of bird species (Meehan et al., 2019) and butterflies (Crossley et al., 2022), the distribution of temperate

¹⁹⁷ trees (Engel et al., 2022) as well as the population dynamics of endangered amphibians (Knapp
¹⁹⁸ et al., 2016) and other ecological processes (Beguin et al., 2012).

¹⁹⁹ We estimated global and spatially-varying trends in endophyte prevalence using a joint-
²⁰⁰ likelihood model. For each host species h , endophyte presence/absence of the i^{th} specimen ($P_{[h]i}$)
²⁰¹ was modeled a Bernoulli response variable with expected probability of endophyte occurrence
²⁰² $\hat{P}_{[h]i}$. We modeled

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

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

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

First, to quantify global trends in endophyte prevalence, we modeled endophyte presence/absences of the i^{th} specimen (P_i) as a Bernoulli response variable with expected probability of endophyte occurrence \hat{P}_i . We modeled \hat{P}_i as a linear function of collection year and accounting for random effects associated with location ($l[i]$, a unique latitude-longitude combination), collector identity ($c[i]$), and scorer identity ($s[i]$) of the i^{th} specimen.

$$\text{logit}(\hat{P}_i) = \alpha_{l[i]} + \beta * \text{year}_i + \chi_{c[i]} + \omega_{s[i]} \quad (2a)$$

²⁰³ Spatially-indexed random intercepts $\alpha_{l[i]}$ account for potential spatial autocorrelation between
²⁰⁴ data points, and year slope β describes the overall temporal trend in endophyte prevalence. We
²⁰⁵ accounted for potential biases introduced during the process of collecting specimens as well as
²⁰⁶ in scoring ability by including random effects specific to each collector χ and scorer ω . Previous
²⁰⁷ work suggests that behavior of historical botanists and uneven sampling may introduce biases
²⁰⁸ into ecological inferences made from historic collections (Kozlov et al., 2020). Prolific collectors
²⁰⁹ who contribute thousands of specimens may be more or less likely to collect certain species,
²¹⁰ or specimens with certain traits (Daru et al., 2018). Similarly, the process of scoring seeds for
²¹¹ hyphae involved several student researchers who, even with standardized training, may vary

212 in their likelihood of positively identifying *Epichloë* hyphae. By including a random effect for
213 collectors and for scorers, we attempted to account for variance across individual researchers
214 that may bias our predictions of changes in endophyte prevalence. Models for each host species
215 were fit separately.⁶ ⁷

Second, to quantify how temporal trends may vary spatially, we repeated the modelling above, but incorporated a spatially-varying coefficient for collection year:

$$\text{logit}(\hat{P}_i) = \alpha_{l[i]} + \beta_{l[i]} * \text{year}_i + \chi_{c[i]} + \omega_{s[i]} \quad (3a)$$

216 The spatially-varying year slope β_l allowed us to flexibly estimate variation in the temporal
217 trajectory of endophyte change at locations across the study region.

218 For both models, spatially-structured random intercepts (α_l) and slopes (β_l) were constructed
219 using stochastic partial differential equations (SPDE) that depend on a covariance matrix accord-
220 ing to the proximity of each collection location (Bakka et al., 2018; Lindgren et al., 2011). The
221 covariance matrix was approximated using a Matérn covariance function, with each data point
222 assigned a location according to the nodes of a mesh of non-overlapping triangles across our
223 study area (Fig A2).⁸

224 We performed model fitting using the inlabru R package (), with vague priors⁹, and compared
225 models with different sizes of mesh, which had little effect on the resulting model estimates¹⁰.
226 Each mesh¹¹ was bounded by the predicted host distribution, described below. Posterior modes
227 were stable¹² indicating that numeric convergence was successful. We assessed model fit with

⁶It would be great to pull all species into one model and have them share variance terms for the random effects. I suspect such a model would give better and more stable estimates.

⁷I updated the notation in ways that make more sense to me, but you should check that this is true to the actual model (I think it is). Also, a more complete presentation of this model would show the variance terms for α , χ , and ω . I presume the latter two are Gaussian but I don't know how to represent the distribution of α .

⁸This paragraph would be a place to describe the variance terms for the other random effects.

⁹I thought you needed informative priors on the spatial decay parameters

¹⁰That's a good but you still need to state what mesh size you used and what that means, biologically.

¹¹You have not defined what you mean by "mesh".

¹²Assessed how?

228 graphical posterior predictive checks (Fig. A3). The model performed adequately at classifying
229 the historical data, comparing the accuracy of predictions from the model with observed data
230 (avg. AUC = 0.77; Fig. A4).¹³

231 *Modeling distributions of host species*

232 We modeled epicloë host species distribution to predict their occurrences in space and time as
233 continuous and binary maps of potential presences. These maps were used as a backbone to
234 predict endophyte prevalence on epicloë host species. The species distribution models were built
235 following the ODMAP (overview, data, model, assessment, prediction) protocol (Crossley et al.,
236 2022). We used the observed presence of the host species collected from GBIF from 1990 to 2020.
237 These occurrences were corrected for spatial autocorrelation due to sampling bias by thinning the
238 occurrences to the spatial scale of the climatic variables. The climatic variables were temperature
239 of the spring, precipitation of the spring and precipitation of the summer. We preferred these
240 variables because they were not correlated (Variance Inflation Factor > 0.7) and also allowed
241 the model to account for the influence of seasonal climate variation on species presence. The
242 occurrence data was split into 75% for model training and 25% for model testing. We fitted
243 the model using maximum entropy (MaxEnt) using the maxent function in the package dismo
244 (Hijmans et al., 2017). MaxEnt was preferred because it does not generate response curves that
245 may cause unpredictable behavior when applied to new climates (Hijmans and Graham, 2006).
246 We used 10000 pseudo-absences as background points. To convert the continuous predicted
247 probabilities into binary presence - absence maps, we used the training sensitivity (true positive
248 rate) and specificity threshold (true negative rate) (Liu et al., 2005). The performances of the
249 model were evaluated using the AUC (Jiménez-Valverde, 2012).

¹³Maybe move this to validation section, and then have both in-sample and out-of-sample approaches.

250

Validating the model with an out-of-sample test

251 We evaluated the predictive ability of the model using contemporary endophyte surveys as out-
 252 of-sample test data, **an important but rarely used strategy in ecological studies** (Tredennick et al.,
 253 2021).¹⁴ We used data from contemporary surveys of endophyte prevalence in *A. hyemalis* and
 254 *E. virginicus* in Texas and the southern US. Surveys of *E. virginicus* were conducted in 2013 as
 255 described in Sneck et al. (2017), and **surveys of *A. hyemalis* took place between 2015 and 2020**¹⁵.
 256 Population surveys of *A. hyemalis* were initially designed to cover longitudinal variation in endo-
 257 phyte prevalence towards its range edge, while surveys of *E. virginicus* were designed to cover
 258 latitudinal variation along its range edge. In total, we visited 43 populations of *A. hyemalis* and 20
 259 populations of *E. virginicus* across the south-central US, with emphasis on Texas and neighboring
 260 states (Fig A4¹⁶). During surveys, we collected seeds from up to 30 individuals per location (av-
 261 erage number of plants sampled: 22.9). We quantified the endophyte status of each individual
 262 with staining microscopy as described for the herbarium surveys (with 5-10 seeds scored per
 263 individual), and calculated the prevalence of endophytes within the population (proportion of
 264 symbiotic plants divided by the number of sampled plants). For each population, we compared
 265 the observed fraction of endophyte-symbiotic hosts to the predicted probability of endophyte oc-
 266 currence \hat{P} derived from the model based on location and year, with collector and scorer random
 267 effects fixed at zero. **The contemporary survey period (2013-2020) is at the most recent edge of**
 268 **the time period encompassed by the historical observations used for model fitting.** We compared
 269 **the model's prediction for these locations to the observed population prevalence.**¹⁷

¹⁴This 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.

¹⁵We 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.

¹⁶This is now A6. Good reminder to use the ref function.

¹⁷It is not clear if you are testing model 1 ("global trend") or model 2 ("spatially varying trends").

Assessing the role of climate drivers

271 We assessed how the magnitude of climate change may have driven changes in endophyte preva-
272 lence by assessing correlations between changes in climate and changes in endophyte prevalence
273 predicted from our spatial model at evenly spaced pixels across the study area. We first down-
274 loaded monthly temperature and precipitation rasters from the PRISM climate group (Daly and
275 Bryant, 2013) covering the time period between 1895 and 2020 using the 'prism' R package (Hart
276 and Bell, 2015). Prism provides reconstructions of historic climate variables across the United
277 States by spatially-interpolating weather station data (Di Luzio et al., 2008). We calculated 30-
278 year climate normals for annual and seasonal mean temperature and cumulative precipitation
279 for the recent (1990 to 2020) and historic (1895 to 1925) periods. We used three four-month sea-
280 sons within the year (Spring: January, February, March, April; Summer: May, June, July, August;
281 Autumn: September, October, November, December). This division of seasons allowed us to
282 quantify differences in climate associated with the two "cool" seasons, when we expect our fo-
283 cal species to be most biologically active (*A. hyemalis* flowering phenology: Spring; *E. virginicus*:
284 Spring and Summer; *A. perennans*: Fall). In addition to mean climate conditions, environmental
285 variability itself can influence population dynamics (Tuljapurkar, 1982) and changes in variabil-
286 ity are a key prediction of climate change models (IPCC, 2021; Stocker et al., 2013). Therefore
287 we calculated the coefficient of variation (CV) during each period for each annual and seasonal
288 climate driver as the interannual standard deviation divided by the mean across each 30-year
289 period. We then took the difference between recent and historic periods for the mean and CV for
290 each climate driver (Fig. A5)¹⁸. Because initial analyses indicated a high degree of collinearity
291 between seasonal and annual changes in temperature, we used annual temperature only, along
292 with annual and seasonal precipitation, in the subsequent analysis. All together, this left us with
293 measurements of change in 10 potential climate drivers: the mean and coefficient of variation
294 of annual temperature, as well as the mean and coefficient of variation of cumulative annual

¹⁸This is Figure A7 – Can you make the color scale on these diverging at zero?

295 precipitation, cumulative spring precipitation, cumulative summer precipitation, and cumulative
296 autumn precipitation (Fig A8-A9)¹⁹.

297 To evaluate whether areas that have experienced the greatest changes in endophyte preva-
298 lence (hotspots of endophyte change) are associated with high degrees of change in climate
299 (hotspots of climate change), we modeled spatially varying slopes of endophyte change through
300 time (β_l) as a linear function of environmental covariates, with a Gaussian error distribution.²⁰
301 Calculating correlations from many pixels across the study region risks artificially inflating confi-
302 dence in our results due to large sample sizes, and so we repeated this calculation using only a
303 random subsample of 100 pixels across the study region²¹.²²²³

304 **Results**

305 *How has endophyte prevalence changed over time?*

306 We found that endophyte prevalence increased within the examined specimens over the last
307 two centuries for all three host species (Fig. 4). On average, *A. hyemalis* and *E. virginicus* both
308 increased from 30 % to over 70% prevalence across the study region, and *A. perennans* increased
309 from 15% to over 70% prevalence. Our model indicates a higher certainty that overall temporal
310 trends are positive for *A. hyemalis* and *A. perennans* than for *E. virginicus* (99% probability of a
311 positive overall year slope in *A. hyemalis*, 89% probability of a positive overall year slope in *A.*
312 *perennans*, and 58% probability of a positive overall year slope in *E. virginicus*).²⁴

¹⁹ The species names are not clear on Fig A9. I suggest increase the font siize

²⁰I 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 disgraphution.

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

²²Are the methods above repeated for each species separately?

²³I 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 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.

²⁴These numbers are currently outdated. I am making some adjustments to models, and will update with final model

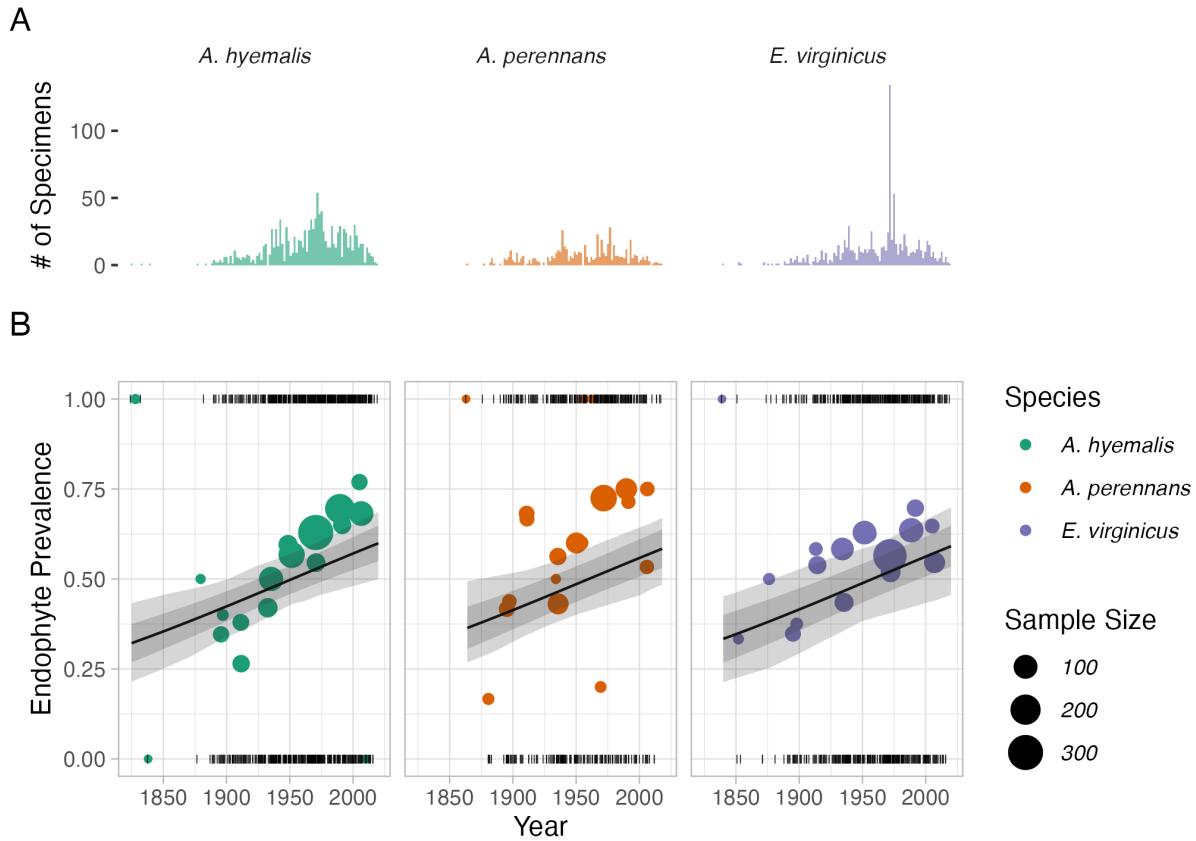


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of collection through time for each host species. (B) Colored points are binned means of the observed endophyte presence/absence data (black dashes). Colors represent each host species and point size is determined by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

313 *How spatially heterogenous are temporal trends in endophyte prevalence?*

314 Our model revealed hotspots of change in endophyte prevalence . While there was an overall
 315 increase in endophyte prevalence, these changes varied across the host species' ranges (Fig. 3).
 316 In some regions, posterior estimates of our spatially varying temporal trends, τ , indicate that *A.*
 317 *hyemalis* and *A. perennans* experienced increases in percent prevalence by as much as 4% per year

318 over the study period, while *E. virginicus* experienced increases up to around 1.5 % per year. In
319 other regions, there were negligible changes. Notably, the symbionts of *E. virginicus* experienced
320 only slight increases in prevalence, and were less spatially variable than the other two species.
321 Regions that start with low endophyte prevalence, as in the southwestern portion of the range
322 of *A. hyemalis*(Fig. A1), also experienced negligible change, suggesting that this may be driven
323 more by the absence of the endophyte.²⁵ Predicted trends for *A. perennans* show certain areas
324 of both large increase and of large decrease, however this species, for which we have the fewest
325 samples, has the largest uncertainty. The posterior estimates of our spatially varying temporal
326 trends, indicate relatively narrow certainty (need to compute²⁶).

²⁵more discussion material, but putting it here for now.

²⁶

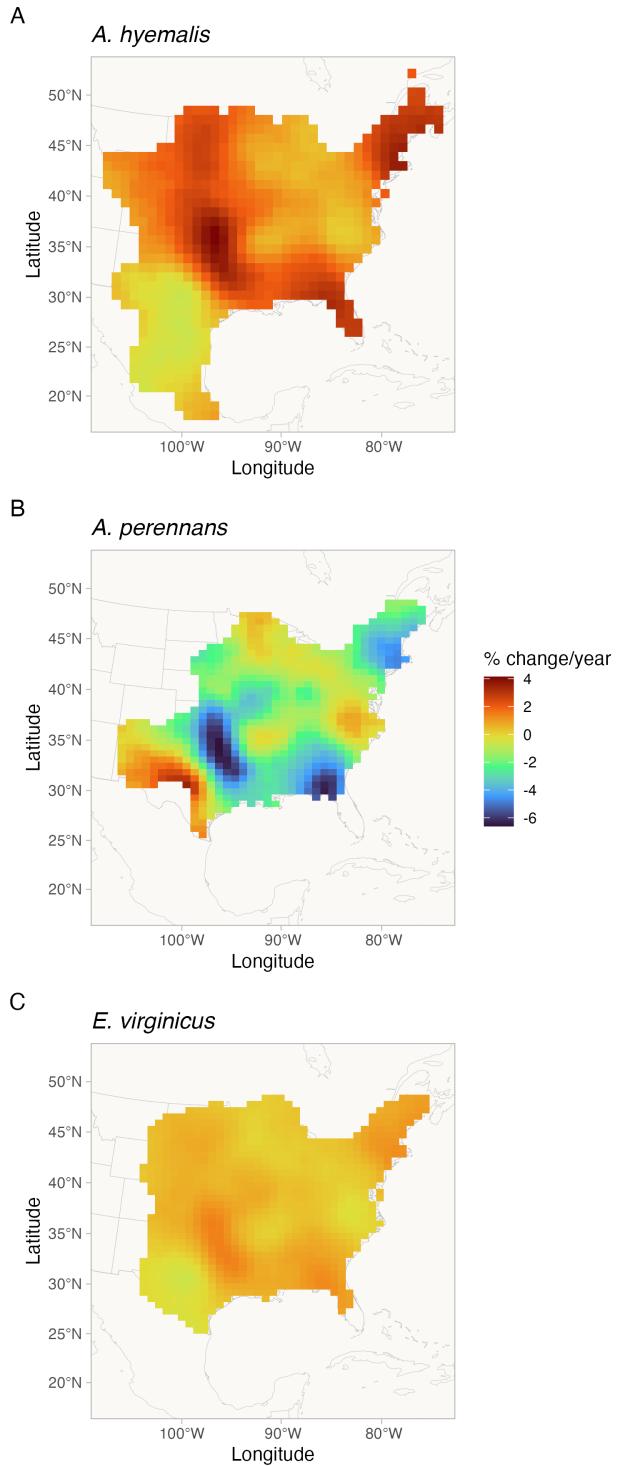


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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

328 We quantified temporal and spatial trends in endophyte prevalence while accounting for poten-
329 tial biases introduced by collectors and by individuals who quantified endophyte presence/absence
330 with the use of random effects. We found no evidence that collector biases influenced our re-
331 sults. Collector random effects were consistently small; Fig 4A, and models fit with and without
332 this random effect provide qualitatively similar results. The identity of individual scorers did
333 contribute to observed patterns in endophyte prevalence. For example, 3 of the 16 scorers were
334 more likely than average to assign positive endophyte status, as indicated by 95% credible in-
335 tervals that do not overlap 0) (Fig 4B). However, this may have been driven by differences in
336 scorers biases during the seed scoring process, or by unintended spatial clustering of the speci-
337 mens scored by each scorer. Interpreting our models with the inclusion of the scorer effect thus
338 provides conservative estimates of the absolute magnitude of changes in endophyte prevalence.

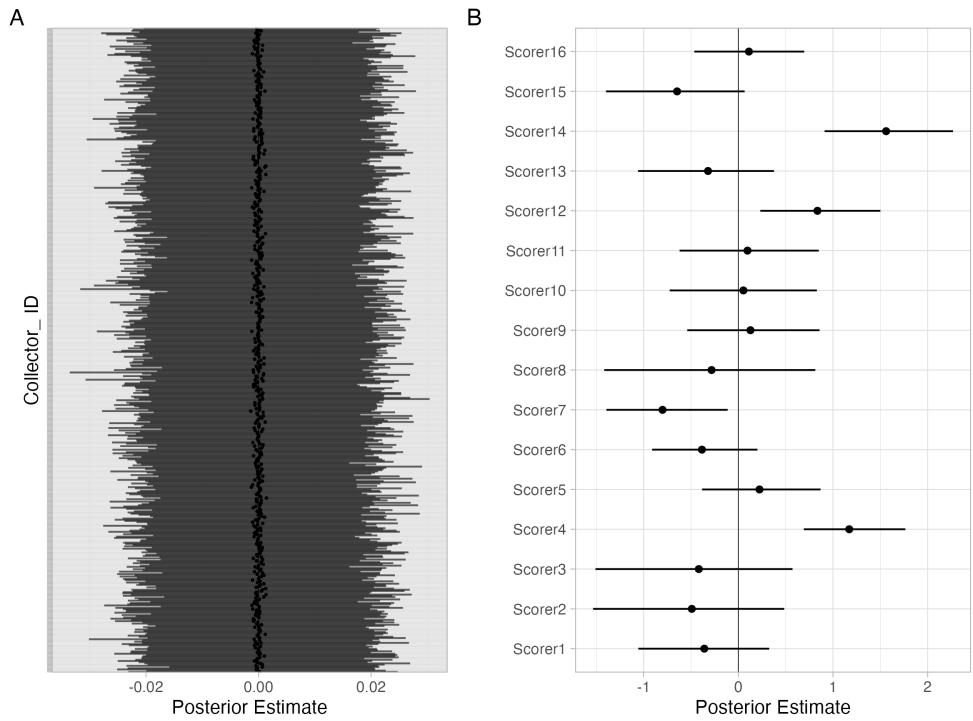


Figure 4: Posterior estimates of (A) collector and (B) scorer random effects. Points show the posterior mean along with 95% CI for random effects estimate from 532 collectors and 16 scorers.

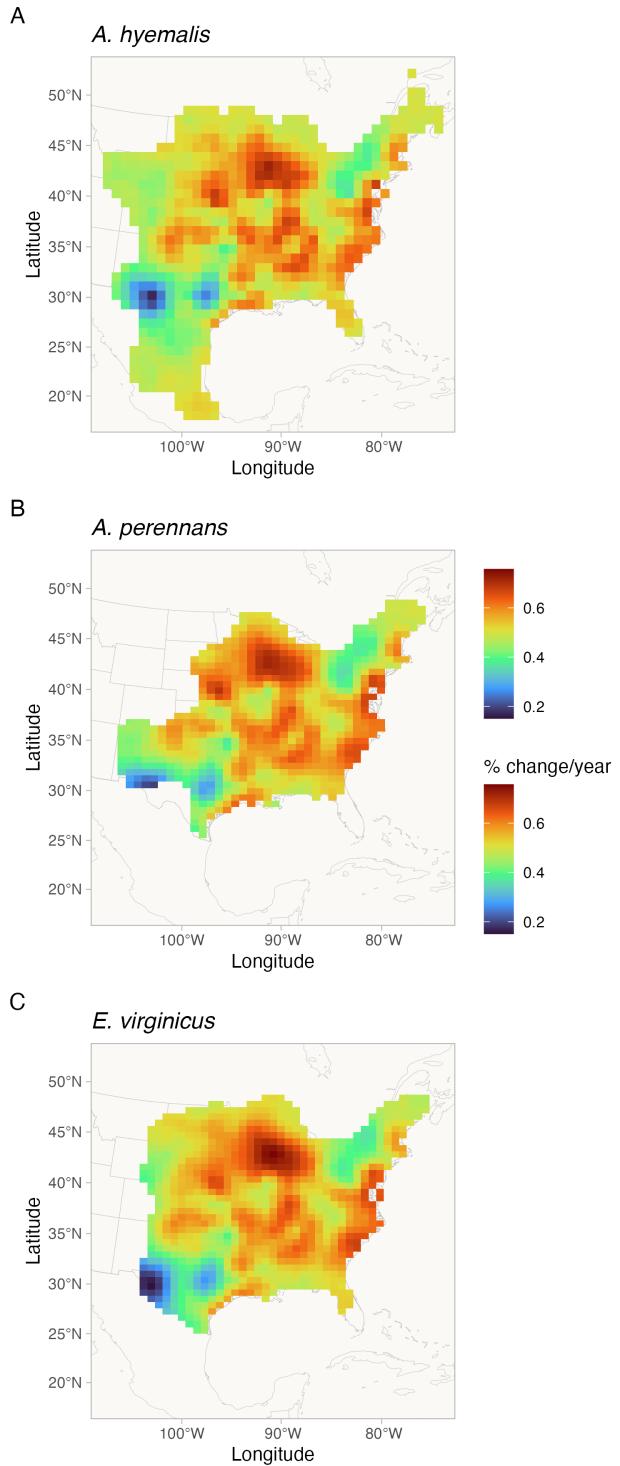


Figure 5: Mean predicted endophyte prevalence for each host species (columns) in 1925 (top row) and 2020 (bottom row). Color indicates mean predicted rate of endophyte prevalence across the predicted distribution of each species.

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

341 We found that trends in endophyte prevalence were strongly associated with seasonal climate
342 change drivers (Fig. 6). For the majority of the study region, the climate has become wetter and
343 cooler over the last century (Fig. A7-A8), a consequence of regional variation in global climate
344 change (IPCC, 2021). Within the study region, spatially heterogeneous environmental changes
345 were predictive of changes in endophyte prevalence. For example, strong increases in prevalence
346 within *E. virginicus* were most associated with declines in Summer precipitation (a negative cor-
347 relation in Fig. 7) as well as with increases in the year-to-year variability of annual temperature
348 (a positive correlation in Fig. 7). Changes were also associated with reductions in average an-
349 nual temperatures, and increases in year-to-year temperature variability. *A. perennans* endophyte
350 prevalence increased most strongly in regions that experienced reduced spring precipitation and
351 reduced variability in annual temperature. Although these correlations were weaker, changes
352 in *A. perennans* endophyte prevalence were also associated with increased in increases in annual
353 precipitation and increasing autumn precipitation. For *A. hyemalis*, endophyte prevalence in-
354 creased most strongly in regions that experienced reductions in autumn precipitation variability.
355 Correlations using only a subsampling of pixels were qualitatively similar to these results (Fig.
356 A11), suggesting that the patterns we find are not spurious associations.

357 27

²⁷Only have plotted results for AGHY right now.

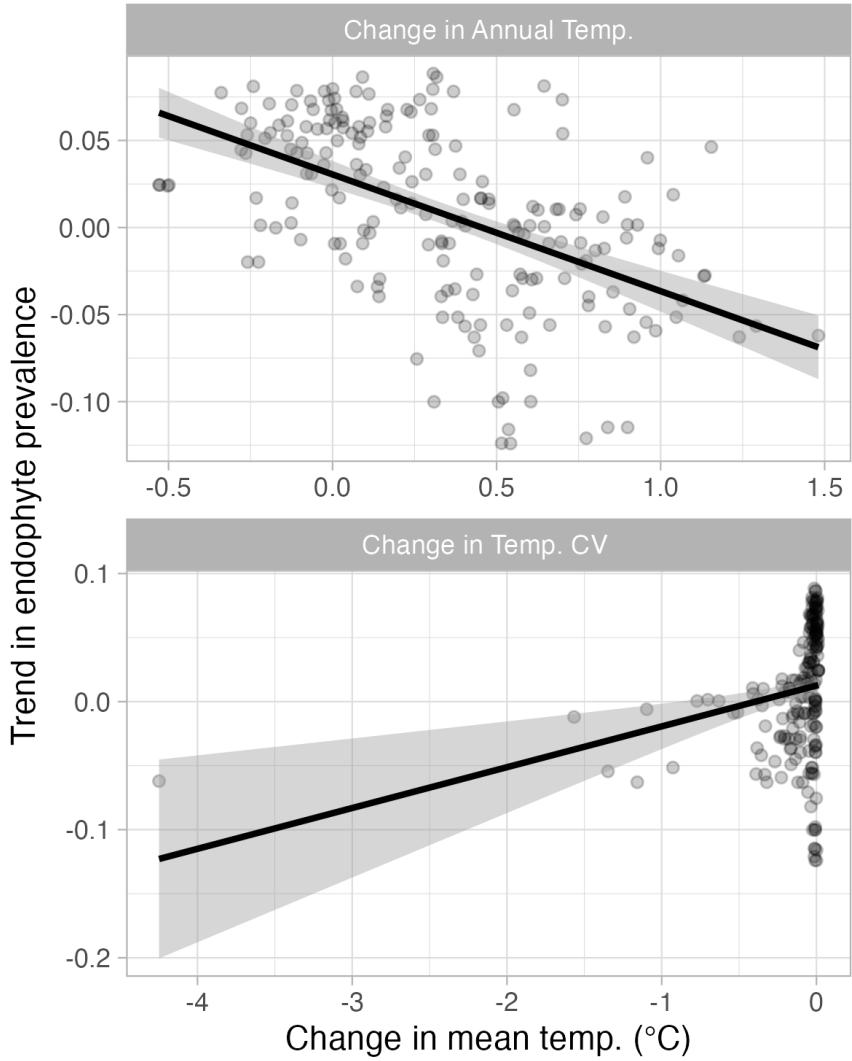


Figure 6: Correlations between changes in climate drivers and changes in endophyte prevalence. Color denotes the Spearman correlation coefficient between the relative rate of change in endophyte prevalence and the change in annual mean temperature ($^{\circ}\text{C}$) and total annual and seasonal precipitation (mm), as well as the change in the coefficient of variation of each climate driver. Positive correlation coefficients indicate that greater increases in a climate driver were associated with larger increases in endophyte prevalence, while negative values indicate that . Asterisks denote correlation coefficients $> .3$ or $< -.3$.

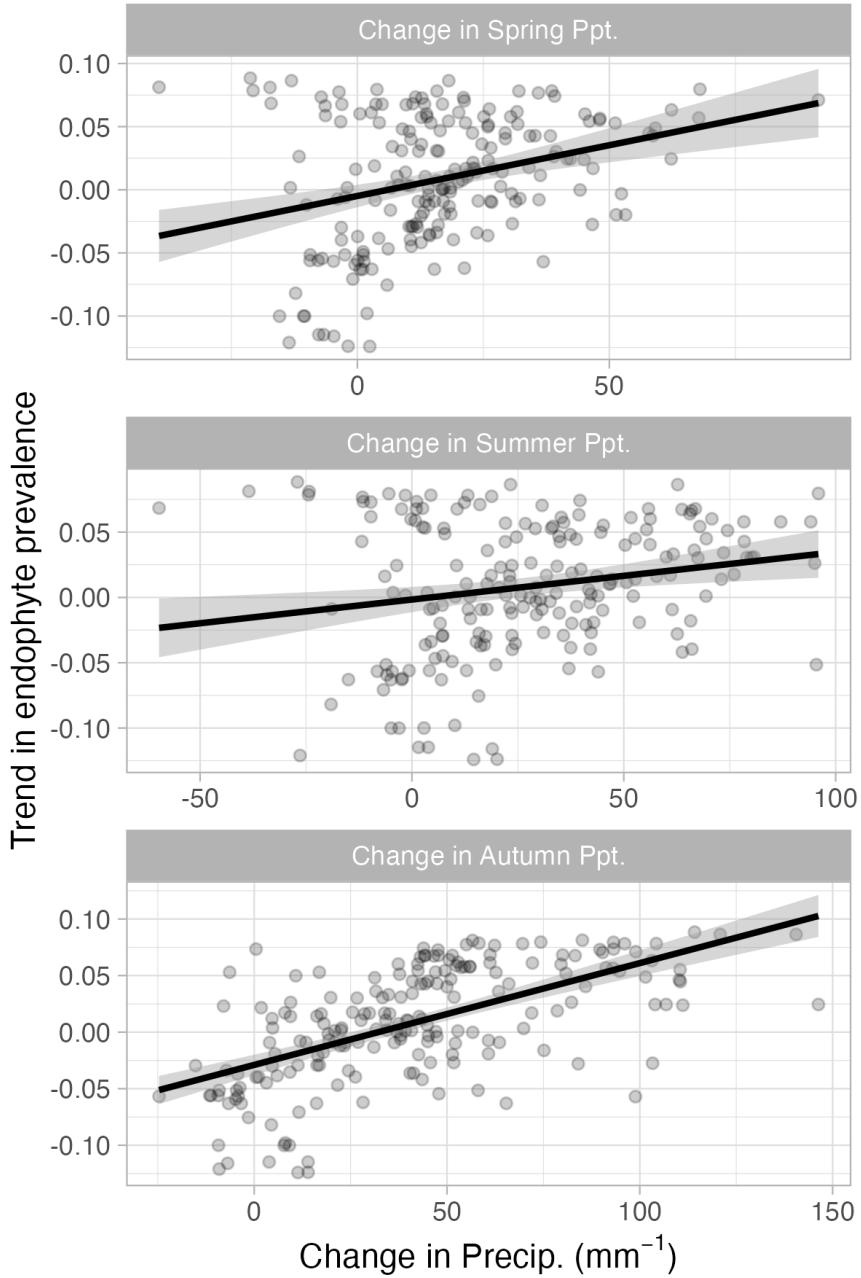


Figure 7: Correlations between changes in climate drivers and changes in endophyte prevalence. Color denotes the Spearman correlation coefficient between the relative rate of change in endophyte prevalence and the change in annual mean temperature ($^{\circ}\text{C}$) and total annual and seasonal precipitation (mm), as well as the change in the coefficient of variation of each climate driver. Positive correlation coefficients indicate that greater increases in a climate driver were associated with larger increases in endophyte prevalence, while negative values indicate that .
 Asterisks denote correlation coefficients $> .3$ or $< -.3$.

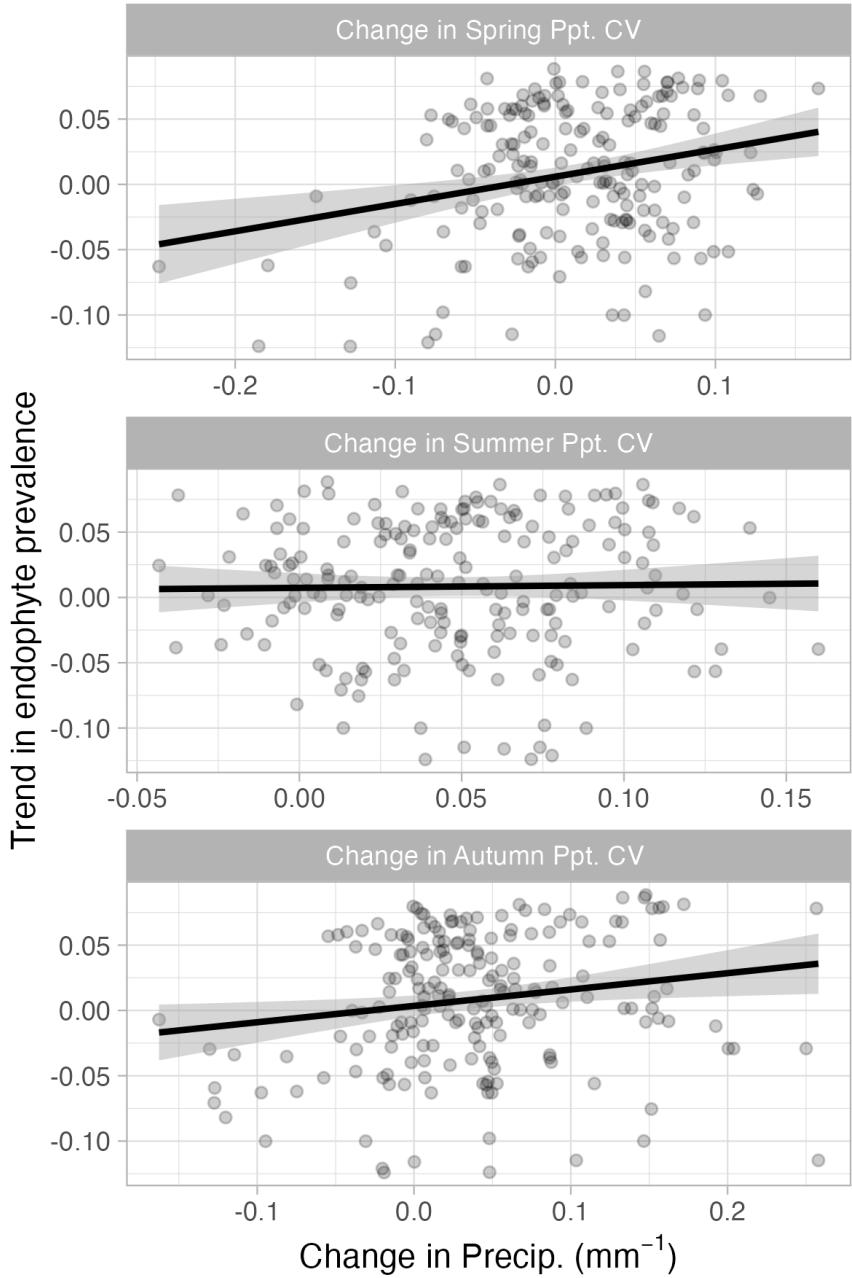


Figure 8: Correlations between changes in climate drivers and changes in endophyte prevalence. Color denotes the Spearman correlation coefficient between the relative rate of change in endophyte prevalence and the change in annual mean temperature ($^{\circ}\text{C}$) and total annual and seasonal precipitation (mm), as well as the change in the coefficient of variation of each climate driver. Positive correlation coefficients indicate that greater increases in a climate driver were associated with larger increases in endophyte prevalence, while negative values indicate that .
25 Asterisks denote correlation coefficients $> .3$ or $< -.3$.

358 *Performance on test data*

359 We found that while the model predicts broader regional trends in endophyte prevalence present
 360 in the contemporary survey data such as declining endophyte prevalence towards western longi-
 361 tudes in *A. hyemalis* (Fig. 6 B-C), however the contemporary data contains additional variability
 362 at smaller scales not captured by our sampling of herbarium specimens. We interpreted this to
 363 mean that the model captured regional spatial dynamics, but underpredicts local scale dynamics.

364 We discuss potential model improvements in the Discussion.

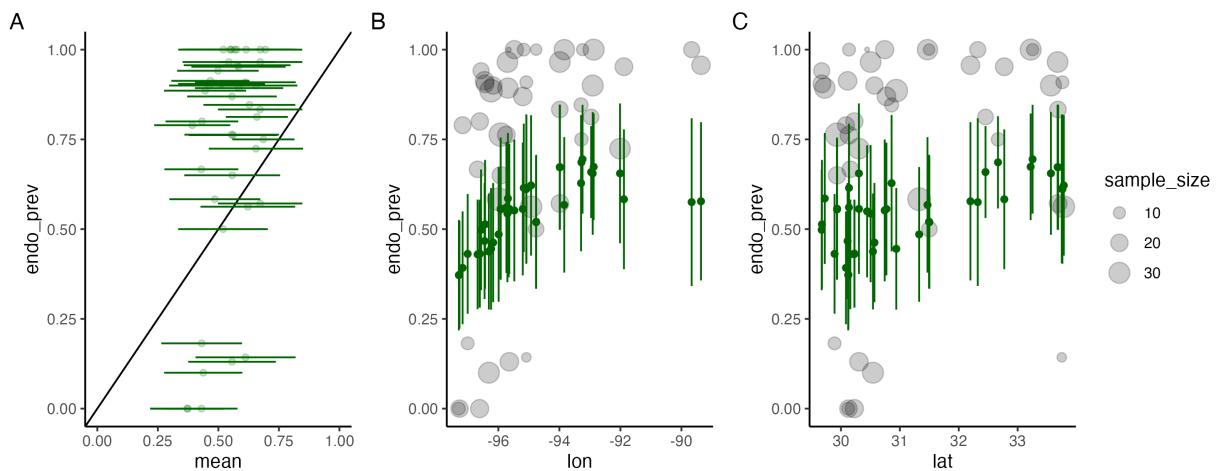


Figure 9: **Predicted vs observed endophyte prevalence for contemporary test data.** (A) The model, trained on historic herbarium collection data, performed modestly at predicting contemporaneous endophyte prevalence in *A. hyemalis*, as indicated by some overlap of predicted 95% CI with the 1:1 line, 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.

Discussion

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

376 Differences between the responses of each host species underscore that while all of these
377 C₃ grasses share similar broad-scale distributions, each engages in unique biotic interactions
378 and has unique niche requirements. We identified hotspots of change for *A. perennans*, which
379 experienced the strongest absolute changes in endophyte prevalence (Fig. 5). Declines in the
380 southern portion of its range and increases in the north suggest a potential poleward range shift
381 of endophytic plants. Based on previous work demonstrating that endophytes can shield their
382 hosts from drought stress (Decunta et al., 2021), we generally predicted that drought conditions
383 could be a driver of increasing endophyte prevalence. In line with this expectation, increas-
384 ing prevalence for this species was associated with decreasing precipitation, most strongly with
385 autumn-season declines (Fig. 7). *A. perennans* typically blooms in the autumn. Endophytes could
386 be playing a role helping hosts weather autumn-season droughts while the species is dormant.
387 It may be useful to investigate whether lagged climate effects are important predictors of host
388 fitness in this system (Evers et al., 2021). To our knowledge, the response of the symbiosis in
389 *A. perennans* to drought has not been examined experimentally, but in a greenhouse experiment,
390 endophytes had a positive effect on host reproduction under shaded, low-light conditions (Davitt

391 et al., 2010). *Epichloë* endophytes have been connected to a suite of non-drought related fitness
392 benefits including herbivore protection (Brem and Leuchtmann, 2001), salinity resistance (Wang
393 et al., 2020), and mediation of the soil microbiome (Roberts and Ferraro, 2015) These effects are
394 potentially mediated by the diverse bioactive alkaloids and other signaling compounds they pro-
395 duce (Saikkonen et al., 2013). The strong increase in symbiotic *A. perennans* could be explained,
396 at least in part, by these diverse benefits. *A. hyemalis* experienced more consistently positive in-
397 creases in endophyte prevalence related to changes in spring temperature and precipitation. This
398 result is in line with previous work demonstrating drought benefits in a greenhouse manipula-
399 tion with this species (Davitt et al., 2011) that led us to expect that endophyte prevalence should
400 similarly increase at a greater rate in regions that have experienced increasing drought. For *E.*
401 *virginicus*, which experienced the most modest changes in endophyte prevalence overall, we found
402 a strong relationship between temporal trends and changes in the mean and variability of tem-
403 perature, as well as with decreases in summer precipitation. Surveys by Sneck et al. (2017), used
404 as part of the test data in this study, identified a drought index (SPEI) that integrates precipitation
405 with estimated evapotranspiration as an important predictor of endophyte prevalence. While we
406 show consistent increasing trends in prevalence between the three species, the mechanisms that
407 explain these changes may be diverse and idiosyncratic.

408 Our spatially-explicit model predicted regions of both high and low endophyte prevalence,
409 suggesting that symbiotic and non-symbiotic host plants have overlapping, but non-identical
410 niche requirements. Endophytes fitness benefits potentially explain the spatial distribution of
411 prevalence by allowing their hosts to persist in environments where they otherwise could not
412 (Afkhami et al., 2014; Kazenel et al., 2015). For example, fitness benefits of the symbiosis could
413 explain high predicted prevalence in *E. virginicus* towards the north or in *A. hyemalis* towards
414 its range center coinciding with strong environmental gradients. Previous population surveys
415 for endophytes, which were used as test data for our model, found similar latitudinal trends
416 in prevalence in these species (Rudgers and Swafford, 2009; Sneck et al., 2017), but at smaller
417 scales. While the model recreated these large-scale spatial trends, test data was more variable.

418 Using test data to validate our model predictions allows us to evaluate places to improve the
419 model's ability to perform well at out-of-sample prediction, which will be particularly important
420 for predicting host and symbiont niche-shifts under future climate change. Lack of information
421 on local variability may simply be a feature of data derived from herbarium specimens. Even
422 though they are samples from local populations, they are single specimens that are aggregated
423 over in broad-scale model estimates. Poor predictive ability at local scales in this grass-endophyte
424 system is not surprising, as previous studies have found that local variation, even to the scale of
425 hundreds of meters can structure endophyte-host niches (Kazenel et al., 2015). Sneck et al. (2017)
426 also identified host genotype as an important predictor of endophyte prevalence in *E. virginicus*.
427 Other studies have found factors including land-use history (Vikuk et al., 2019) and the biotic
428 environment, including herbivory (Rudgers et al., 2016), to be important predictors of endophyte
429 ecology. Incorporating available climatic and soil layers as covariates is an obvious first step
430 that could improve predictions. Towards the goal of predicting the dynamics of microbial sym-
431 bioses under climate change, models that integrate data from local and regional scales would be
432 an important step to bridge the gap that often exists between large but broad bioclimatic and
433 biodiversity data and small but local data on biotic interactions (Isaac et al., 2020; Miller et al.,
434 2019).

435 Our analysis advances the use of herbarium specimens in global change biology in two ways.
436 First and foremost, this is the first study to link long-term changes in microbial symbioses to
437 changes in climate using specimens from natural history collections. The responses of micro-
438 bial symbioses are a rich target for future studies within museum specimens, particularly those
439 that take advantage of advances in sequencing technology. While we used relatively coarse
440 presence/absence data based on fungal morphology, other studies have examined historic plant
441 microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these
442 studies have so far been limited to relatively few specimens at limited spatial extents (Bieker
443 et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al.,
444 2015). Continued advances in capturing historic DNA and in filtering out potential contami-

445 nation during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith,
446 2021) will be imperative in the effort to scale up these efforts. This scaling up will be essential
447 to be able to quantify changes not just in the prevalence of symbionts, but also in symbionts'
448 intraspecific variation and evolutionary responses to climate change, as well as in changes in the
449 wider microbial community. Answering these questions as well as the unknown questions that
450 future researchers may ask also reiterates the value in capturing meta-information during ongo-
451 ing digitization efforts at herbaria around the world and during the accession of newly collected
452 specimens (Lendemer et al., 2020). Second, we accounted for several potential biases in the data
453 observation process that may be common to many collections-based research questions by using
454 a spatially-explicit random effects model. Spatial autocorrelation (Willems et al., 2022), potential
455 biases introduced by the sampling habits of collectors (Daru et al., 2018), and variation between
456 contemporary researchers during the collection of trait data, if not corrected for could lead to
457 over-confident inference about the strength and direction of historic change. Previous studies
458 that have quantified the effects of collector biases typically find them to be small (Davis et al.,
459 2015; Meineke et al., 2019), and we similarly did not find that collector has a strong effect on the
460 results of our analysis. Fitting this model in a Bayesian framework allows for full propagation of
461 uncertainty.

462 Ultimately, a central goal of global change biology is to generate predictive insights into the
463 future of natural systems. While this survey of historic endophyte prevalence is necessarily cor-
464 relative, it serves as a foundation to develop better predictive models of the response of microbial
465 symbioses to climate change. Combining the insights from this type of regional-scale survey with
466 field experiments and physiological data could be invaluable. While we found that climate is
467 strongly correlated with endophytes' temporal responses, we do not know why trends in preva-
468 lence were weak in some areas or how endophytes would respond to more extreme changes in
469 climate. For example, transplanting symbiotic and non-symbiotic plants beyond the range edge
470 of *A. hyemalis* could tell us whether persistent low endophyte prevalence in that area is a result of
471 environmental conditions that lead the symbiosis to negative fitness consequences, or is a result

472 of some historical contingency or dispersal limitation that has thus far limited the presence of
473 symbiotic hosts from a region where they would otherwise flourish and provide resilience. While
474 we observed evidence of mutualism resilience, more extreme environmental changes than those
475 observed in our study could potentially push one or both partners beyond their physiological
476 limit, leading to the collapse of the mutualism. Our analysis thus far is agnostic to changes in the
477 distributions of hosts. Mechanistic models could connect the responses of both host and sym-
478 bionts to abiotic climate drivers integrating dispersal processes. Beyond host-microbe symbioses,
479 building these types of models would work towards quantitatively attributing biotic responses
480 to anthropogenically driven climate change, similar to methods in climate science and economics
481 (Carleton and Hsiang, 2016; Stott et al., 2010).

482 Acknowledgments

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

491 Statement of Authorship

492 Data and Code Availability

493 On initial submission, you may use this section to provide a URL for editors and reviewers that
494 is ‘private for peer review’. After acceptance, this section must be updated with correct, working

⁴⁹⁵ DOIs for data deposits (typically on the Dryad Digital Repository,) and code deposits (such as
⁴⁹⁶ in Zenodo).

⁴⁹⁷

Appendix A

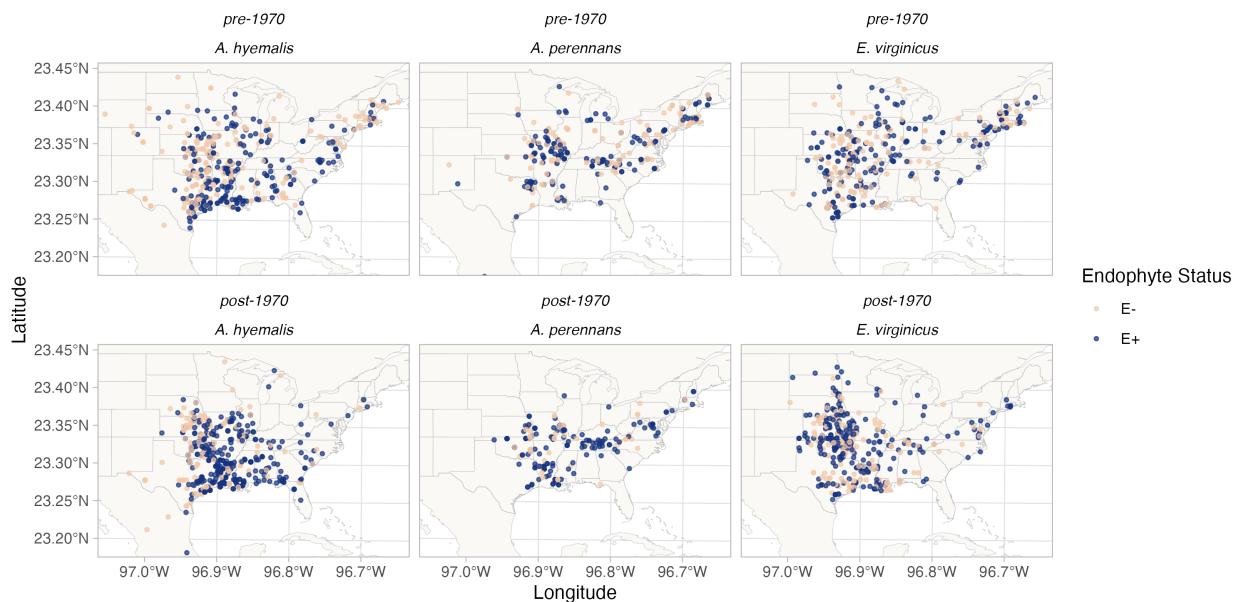


Figure A1: **Endophyte presence/absence in specimens of each host species.** Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points) and are faceted based on collection period.

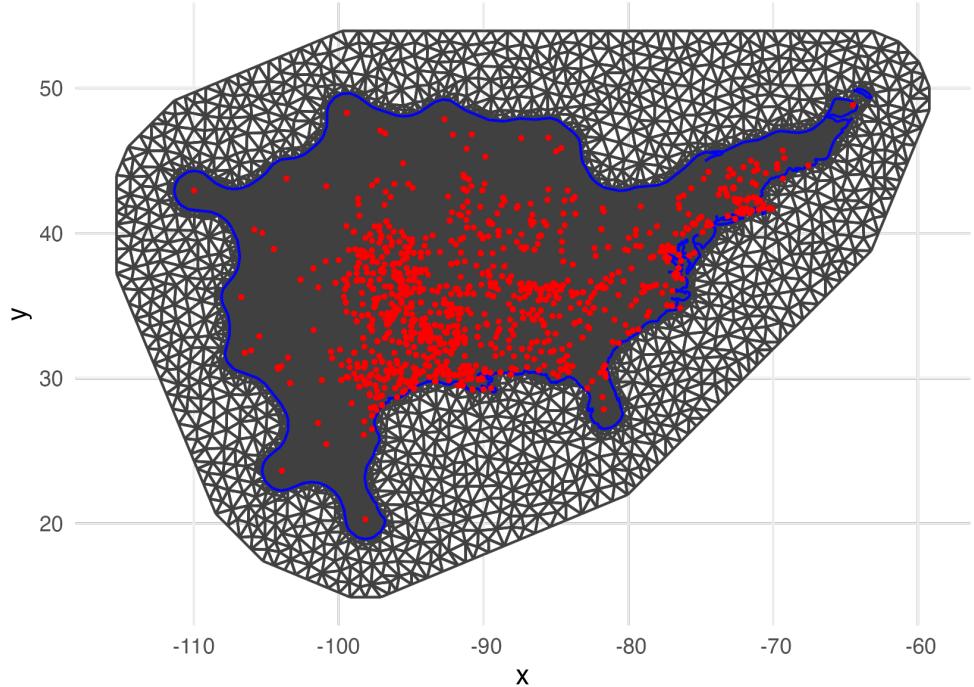


Figure A2: Delauney triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Red points indicate locations of sampled herbarium specimens, and the blue outlines show the international borders used to define the edge of the mesh along coastlines.

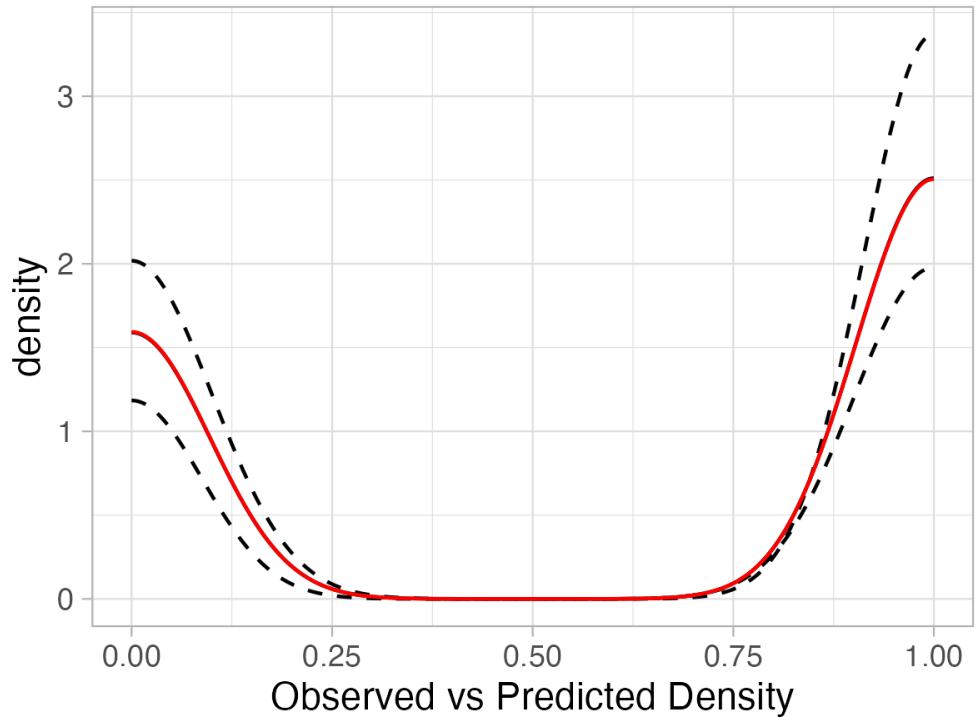


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (red) along with the mean(solid) and 95% CI (dashed) of simulated values (black).

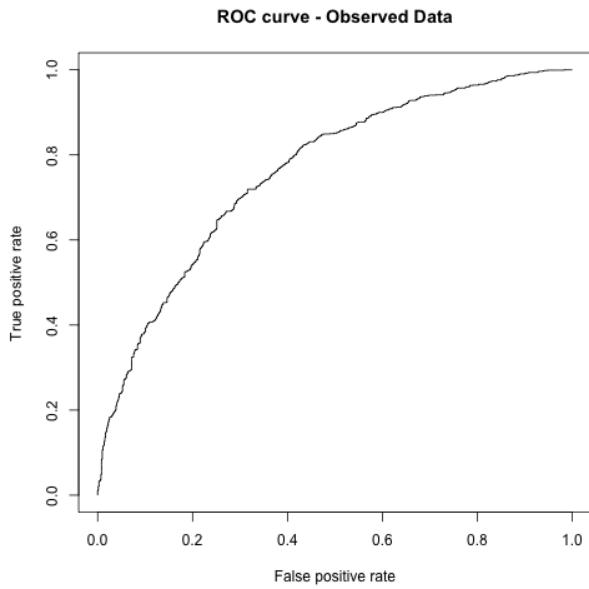


Figure A4: ROC plot showing model performance classifying observations according to endophyte status. The curves show adequate model performance for observed (top) and test (bottom) data. The AUC for each is 0.77.

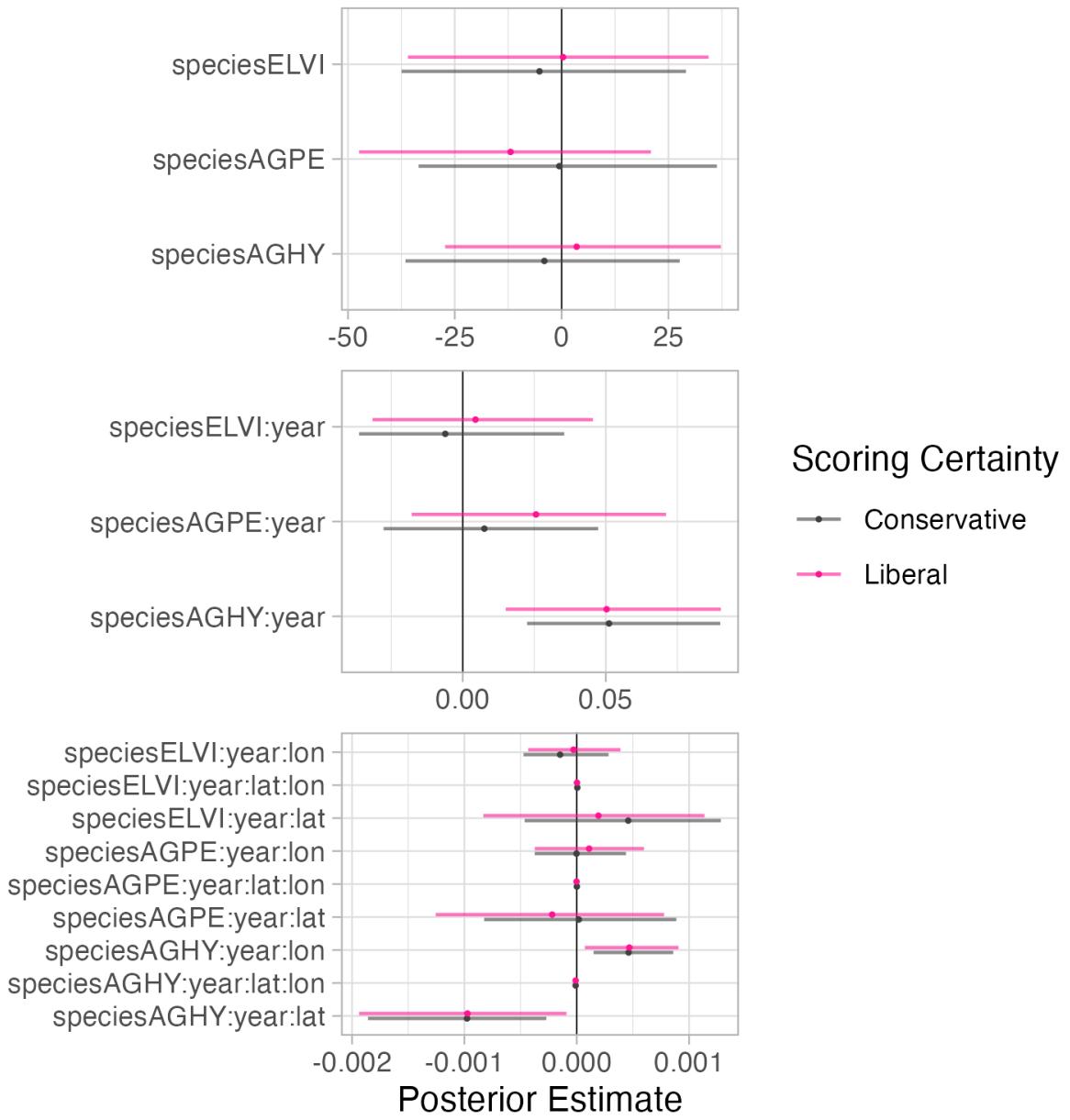


Figure A5: Comparison of posterior estimates of fixed effects when using Liberal or Conservative endophyte scores.

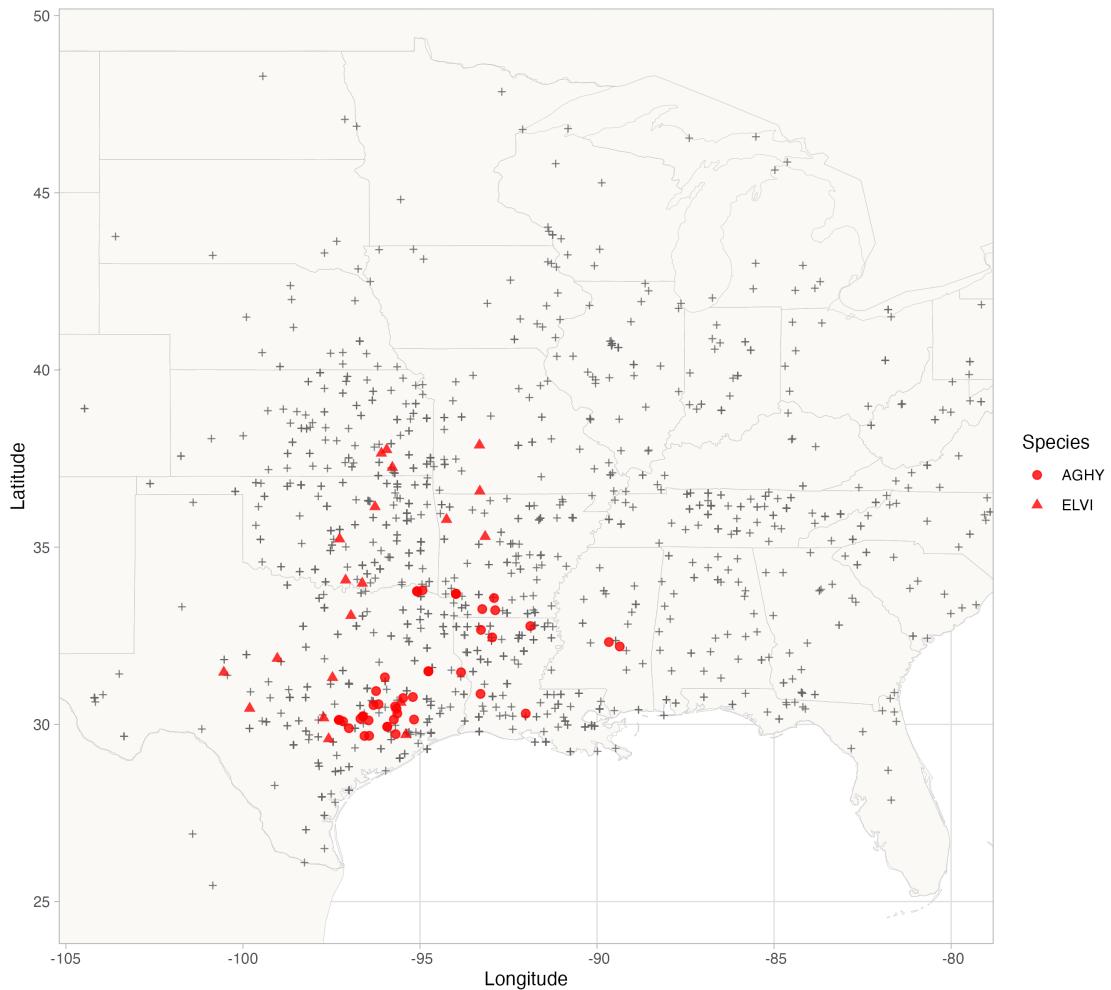


Figure A6: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

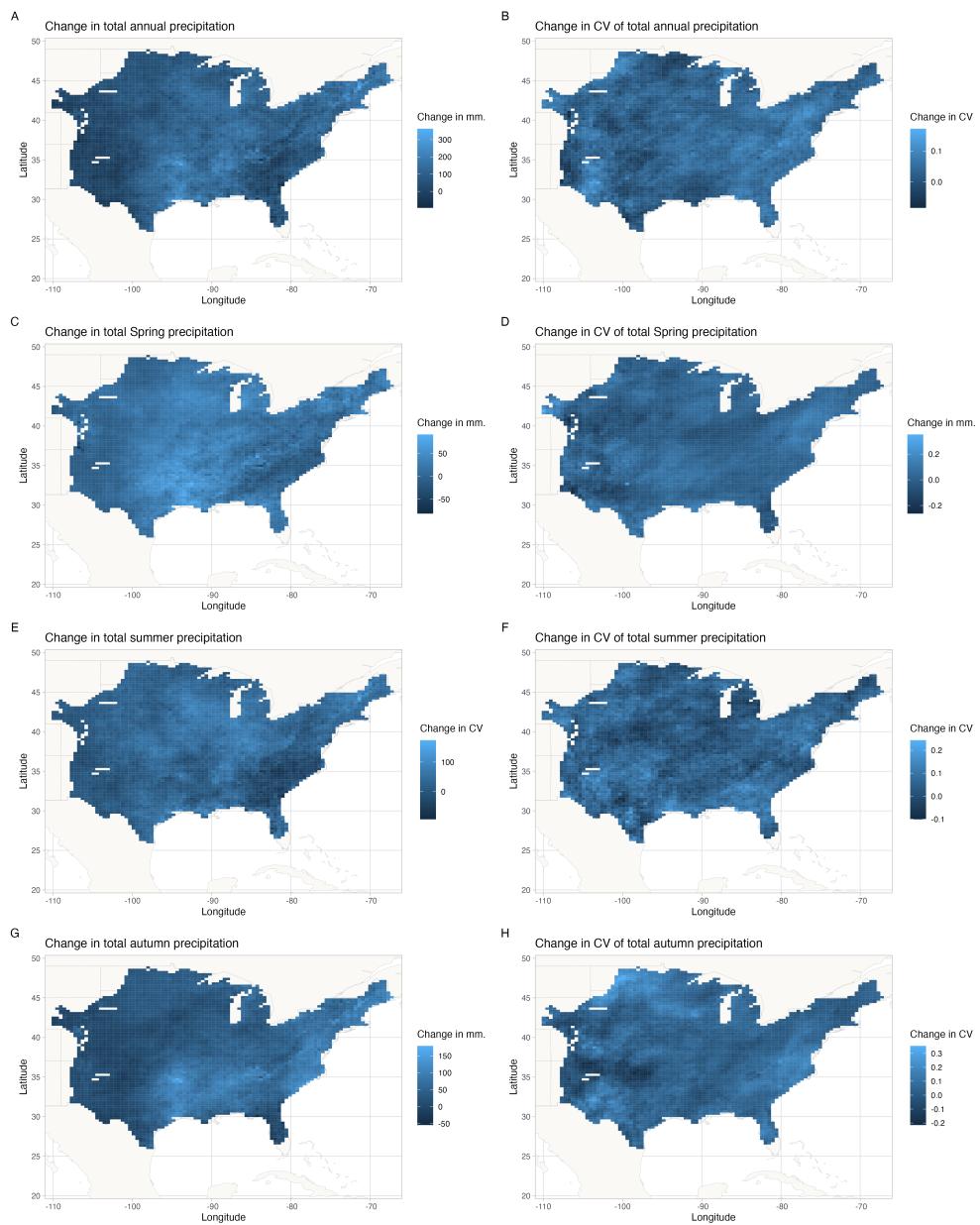


Figure A7: Change in precipitation between the periods 1895-1925 and 1990-2020. Color represents change in annual or seasonal total precipitation (A,C,E,G) and in the coefficient of variation of annual or seasonal total precipitation (B,D,F,H). Maps show the study area of *A. hyemalis*. Map pixels used in correlation analysis with endophyte change were pulled from studies areas specific to each host species.

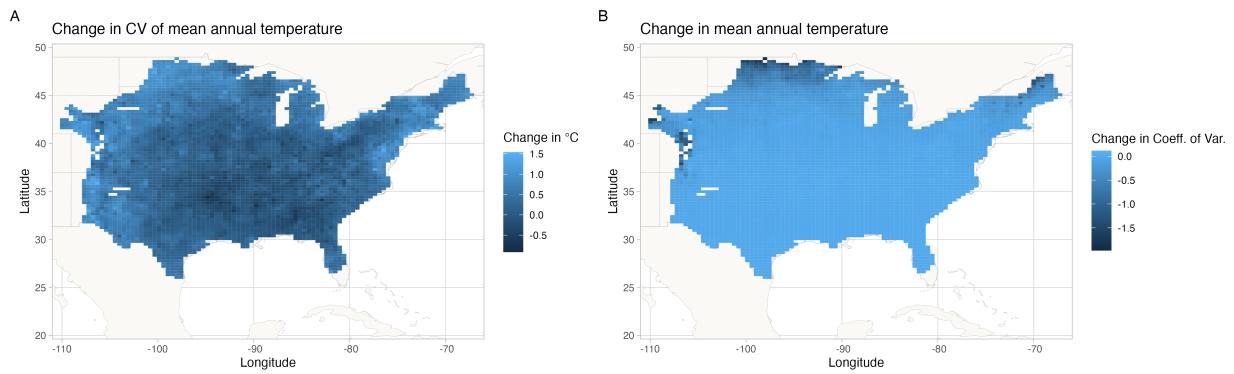


Figure A8: Change in temperature between the periods 1895-1925 and 1990-2020. Color represents change in annual mean temperature (A) and in the coefficient of variation of annual mean temperature (B). Maps show the study area of *A. hyemalis*. Map pixels used in correlation analysis with endophyte change were pulled from studies areas specific to each host species.

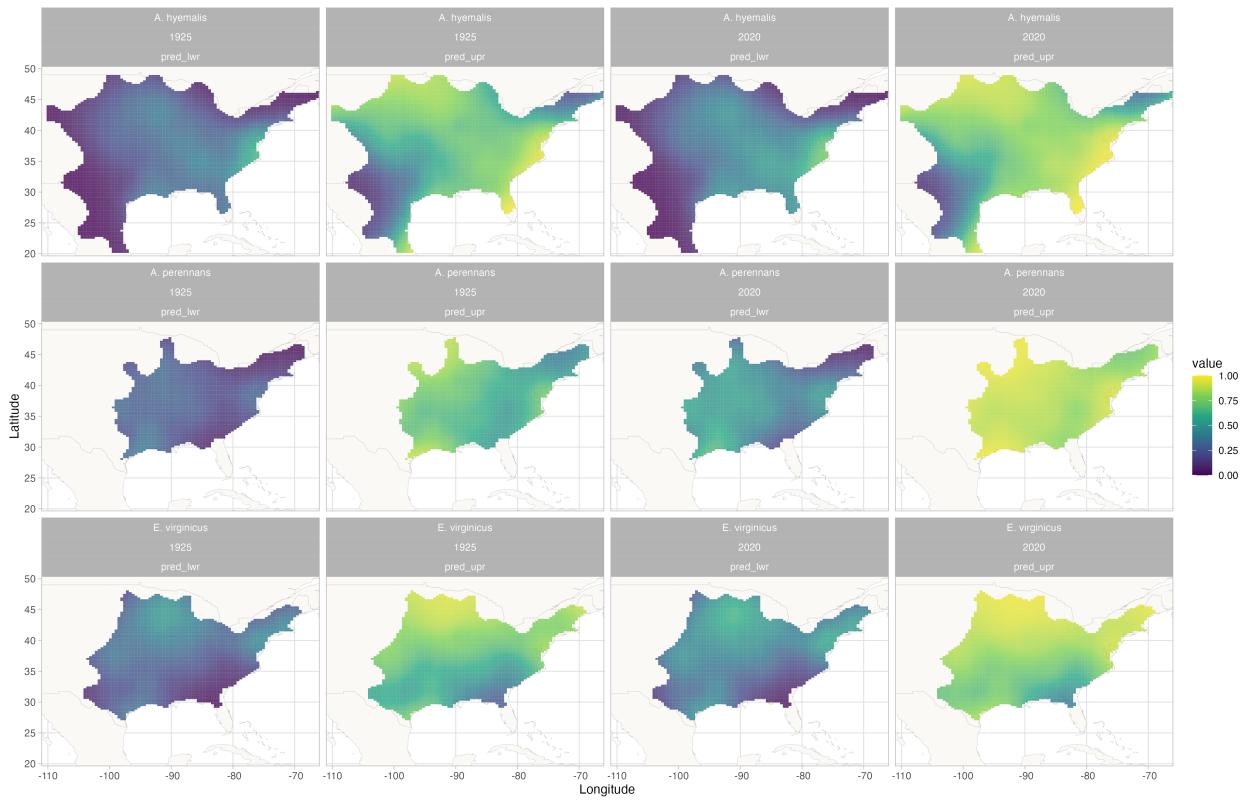


Figure A9: Uncertainty associated with spatial trends in endophyte prevalence. Color represents change in predicted endophyte prevalence. Panels show upper and lower 95% posterior probability for each host species between 1925 and 2020.

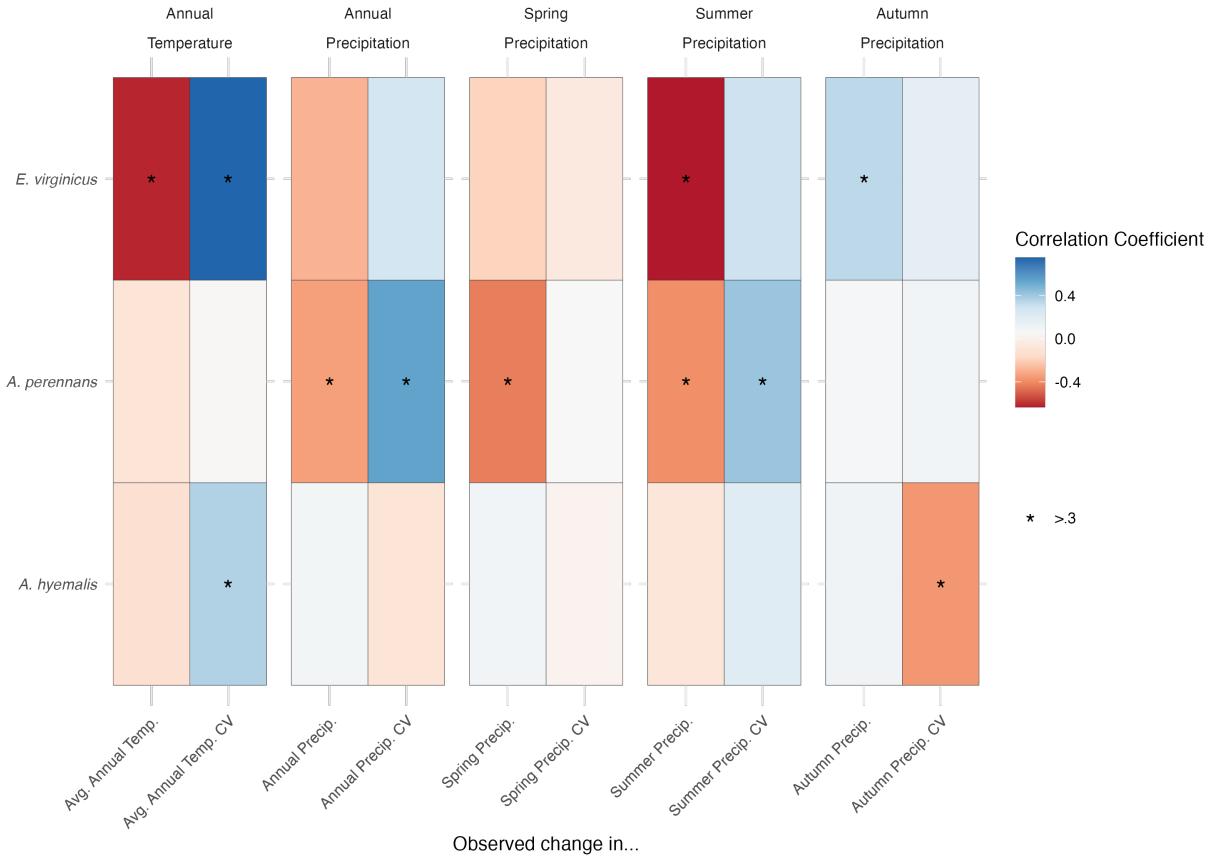


Figure A10: Correlations between changes in climate drivers and changes in endophyte prevalence from a random sample of 100 pixels across the study region. Color denotes the Spearman correlation coefficient between the relative rate of change in endophyte prevalence and the change in annual mean temperature ($^{\circ}\text{C}$) and total annual and seasonal precipitation (mm), as well as the change in the coefficient of variation of each climate driver. Positive correlation coefficients indicate that greater increases in a climate driver were associated with larger increases in endophyte prevalence, while negative values indicate that . Asterisks denote correlation coefficients $> .3$ or $< -.3$.

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

498 Literature Cited

- 499 498 Michelle E Afkhami. Fungal endophyte–grass symbioses are rare in the California floristic
 500 province and other regions with mediterranean-influenced climates. *Fungal ecology*, 5(3):345–
 501 352, 2012.
- 502 Michelle E Afkhami and Jennifer A Rudgers. Symbiosis lost: imperfect vertical transmission of
 503 fungal endophytes in grasses. *The American Naturalist*, 172(3):405–416, 2008.
- 504 Michelle E Afkhami, Patrick J McIntyre, and Sharon Y Strauss. Mutualist-mediated effects on
 505 species' range limits across large geographic scales. *Ecology letters*, 17(10):1265–1273, 2014.
- 506 Sally N Aitken, Sam Yeaman, Jason A Holliday, Tongli Wang, and Sierra Curtis-McLane. Adap-
 507 tation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary
 508 applications*, 1(1):95–111, 2008.

- 509 Clare E Aslan, Erika S Zavaleta, Bernie Tershay, and Donald Croll. Mutualism disruption threatens
510 global plant biodiversity: a systematic review. *PLoS one*, 8(6):e66993, 2013.
- 511 Charles W Bacon and James F White. Stains, media, and procedures for analyzing endophytes.
512 In *Biotechnology of endophytic fungi of grasses*, pages 47–56. CRC Press, 2018.
- 513 Haakon Bakka, Håvard Rue, Geir-Arne Fuglstad, Andrea Riebler, David Bolin, Janine Illian, Elias
514 Krainski, Daniel Simpson, and Finn Lindgren. Spatial modeling with r-inla: A review. *Wiley
515 Interdisciplinary Reviews: Computational Statistics*, 10(6):e1443, 2018.
- 516 Freek T Bakker, Vanessa C Bieker, and Michael D Martin. Herbarium collection-based plant
517 evolutionary genetics and genomics, 2020.
- 518 Dawn R Bazely, John P Ball, Mark Vicari, Andrew J Tanentzap, Myrtille Bérenger, Tomo Rako-
519 cevic, and Saewan Koh. Broad-scale geographic patterns in the distribution of vertically-
520 transmitted, asexual endophytes in four naturally-occurring grasses in sweden. *Ecography*,
521 30(3):367–374, 2007.
- 522 Julien Beguin, Sara Martino, Håvard Rue, and Steven G Cumming. Hierarchical analysis of
523 spatially autocorrelated ecological data using integrated nested laplace approximation. *Methods
524 in Ecology and Evolution*, 3(5):921–929, 2012.
- 525 Colette S Berg, Jason L Brown, and Jennifer J Weber. An examination of climate-driven flowering-
526 time shifts at large spatial scales over 153 years in a common weedy annual. *American Journal
527 of Botany*, 106(11):1435–1443, 2019.
- 528 Vanessa C Bieker, Fátima Sánchez Barreiro, Jacob A Rasmussen, Marie Brunier, Nathan Wales,
529 and Michael D Martin. Metagenomic analysis of historical herbarium specimens reveals a
530 postmortem microbial community. *Molecular ecology resources*, 20(5):1206–1219, 2020.
- 531 Jessica L Blois, Phoebe L Zarnetske, Matthew C Fitzpatrick, and Seth Finnegan. Climate change
532 and the past, present, and future of biotic interactions. *Science*, 341(6145):499–504, 2013.

- 533 Michael Bradshaw, Uwe Braun, Marianne Elliott, Julia Kruse, Shu-Yan Liu, Guanxiu Guan, and
534 Patrick Tobin. A global genetic analysis of herbarium specimens reveals the invasion dynamics
535 of an introduced plant pathogen. *Fungal Biology*, 125(8):585–595, 2021.
- 536 D Brem and A Leuchtmann. Epichloë grass endophytes increase herbivore resistance in the
537 woodland grass *brachypodium sylvaticum*. *Oecologia*, 126(4):522–530, 2001.
- 538 Tamara A Carleton and Solomon M Hsiang. Social and economic impacts of climate. *Science*, 353
539 (6304):aad9837, 2016.
- 540 Shen Cheng, Ying-Ning Zou, Kamil Kuča, Abeer Hashem, Elsayed Fathi Abd Allah, and Qiang-
541 Sheng Wu. Elucidating the mechanisms underlying enhanced drought tolerance in plants
542 mediated by arbuscular mycorrhizal fungi. *Frontiers in Microbiology*, 12:4029, 2021.
- 543 Keith Clay and Christopher Schardl. Evolutionary origins and ecological consequences of endo-
544 phyte symbiosis with grasses. *the american naturalist*, 160(S4):S99–S127, 2002.
- 545 KD Craven, PTW Hsiau, A Leuchtmann, W Hollin, and CL Schardl. Multigene phylogeny of
546 epichloë species, fungal symbionts of grasses. *Annals of the Missouri Botanical Garden*, pages
547 14–34, 2001.
- 548 Kerri M Crawford, John M Land, and Jennifer A Rudgers. Fungal endophytes of native grasses
549 decrease insect herbivore preference and performance. *Oecologia*, 164:431–444, 2010.
- 550 Michael S Crossley, Timothy D Meehan, Matthew D Moran, Jeffrey Glassberg, William E Snyder,
551 and Andrew K Davis. Opposing global change drivers counterbalance trends in breeding north
552 american monarch butterflies. *Global change biology*, 28(15):4726–4735, 2022.
- 553 Christopher Daly and Kirk Bryant. The prism climate and weather system—an introduction.
554 *Corvallis, OR: PRISM climate group*, 2, 2013.
- 555 Barnabas H Daru, Daniel S Park, Richard B Primack, Charles G Willis, David S Barrington,
556 Timothy JS Whitfeld, Tristram G Seidler, Patrick W Sweeney, David R Foster, Aaron M Ellison,

- 557 et al. Widespread sampling biases in herbaria revealed from large-scale digitization. *New*
558 *Phytologist*, 217(2):939–955, 2018.
- 559 Barnabas H Daru, Elizabeth A Bowman, Donald H Pfister, and A Elizabeth Arnold. A novel proof
560 of concept for capturing the diversity of endophytic fungi preserved in herbarium specimens.
561 *Philosophical Transactions of the Royal Society B*, 374(1763):20170395, 2019.
- 562 Charles C Davis, Charles G Willis, Bryan Connolly, Courtland Kelly, and Aaron M Ellison.
563 Herbarium records are reliable sources of phenological change driven by climate and pro-
564 vide novel insights into species' phenological cueing mechanisms. *American journal of botany*,
565 102(10):1599–1609, 2015.
- 566 Andrew J Davitt, Marcus Stansberry, and Jennifer A Rudgers. Do the costs and benefits of fungal
567 endophyte symbiosis vary with light availability? *New Phytologist*, 188(3):824–834, 2010.
- 568 Andrew J Davitt, Chris Chen, and Jennifer A Rudgers. Understanding context-dependency in
569 plant–microbe symbiosis: the influence of abiotic and biotic contexts on host fitness and the
570 rate of symbiont transmission. *Environmental and Experimental Botany*, 71(2):137–145, 2011.
- 571 Facundo A Decunta, Luis I Pérez, Dariusz P Malinowski, Marco A Molina-Montenegro, and
572 Pedro E Gundel. A systematic review on the effects of epichloë fungal endophytes on drought
573 tolerance in cool-season grasses. *Frontiers in plant science*, 12:644731, 2021.
- 574 Mauro Di Luzio, Gregory L Johnson, Christopher Daly, Jon K Eischeid, and Jeffrey G Arnold.
575 Constructing retrospective gridded daily precipitation and temperature datasets for the con-
576 terminous united states. *Journal of Applied Meteorology and Climatology*, 47(2):475–497, 2008.
- 577 Marion L Donald, Teresa F Bohner, Kory M Kolis, R Alan Shadow, Jennifer A Rudgers, and
578 Tom EX Miller. Context-dependent variability in the population prevalence and individual
579 fitness effects of plant–fungal symbiosis. *Journal of Ecology*, 109(2):847–859, 2021.

- 580 AE Douglas. Host benefit and the evolution of specialization in symbiosis. *Heredity*, 81(6):599–
581 603, 1998.
- 582 Yuan-Wen Duan, Haibao Ren, Tao Li, Lin-Lin Wang, Zhi-Qiang Zhang, Yan-Li Tu, and Yong-Ping
583 Yang. A century of pollination success revealed by herbarium specimens of seed pods. *New*
584 *Phytologist*, 224(4):1512–1517, 2019.
- 585 Markus Engel, Tobias Mette, and Wolfgang Falk. Spatial species distribution models: Using
586 bayes inference with inla and spde to improve the tree species choice for important european
587 tree species. *Forest Ecology and Management*, 507:119983, 2022.
- 588 Sanne M Evers, Tiffany M Knight, David W Inouye, Tom EX Miller, Roberto Salguero-Gómez,
589 Amy M Iler, and Aldo Compagnoni. Lagged and dormant season climate better predict plant
590 vital rates than climate during the growing season. *Global Change Biology*, 27(9):1927–1941,
591 2021.
- 592 Paul EM Fine. Vectors and vertical transmission: an epidemiologic perspective. *Annals of the New*
593 *York Academy of Sciences*, 266(1):173–194, 1975.
- 594 Joshua C Fowler, Shaun Ziegler, Kenneth D Whitney, Jennifer A Rudgers, and Tom EX Miller.
595 Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity.
596 *Ecology Letters*, 27(5):e14438, 2024.
- 597 PR Frade, F De Jongh, F Vermeulen, J Van Bleijswijk, and RPM Bak. Variation in symbiont
598 distribution between closely related coral species over large depth ranges. *Molecular Ecology*,
599 17(2):691–703, 2008.
- 600 Sarah E Gilman, Mark C Urban, Joshua Tewksbury, George W Gilchrist, and Robert D Holt. A
601 framework for community interactions under climate change. *Trends in ecology & evolution*, 25
602 (6):325–331, 2010.

- 603 Gustaf Granath, Mark Vicari, Dawn R Bazely, John P Ball, Adriana Puentes, and Tomo Rakoce-
604 vic. Variation in the abundance of fungal endophytes in fescue grasses along altitudinal and
605 grazing gradients. *Ecography*, 30(3):422–430, 2007.
- 606 Andrin Gross, Célia Petitcollin, Cyril Dutech, Bayo Ly, Marie Massot, Julie Faivre d’Arcier, Laure
607 Dubois, Gilles Saint-Jean, and Marie-Laure Desprez-Loustau. Hidden invasion and niche con-
608 traction revealed by herbaria specimens in the fungal complex causing oak powdery mildew
609 in europe. *Biological Invasions*, 23:885–901, 2021.
- 610 Edmund M. Hart and Kendon Bell. prism: Download data from the oregon prism project. 2015.
611 doi: 10.5281/zenodo.33663. URL <https://github.com/ropensci/prism>. R package version
612 0.0.6.
- 613 J Mason Heberling and David J Burke. Utilizing herbarium specimens to quantify historical
614 mycorrhizal communities. *Applications in plant sciences*, 7(4):e01223, 2019.
- 615 Robert J Hijmans and Catherine H Graham. The ability of climate envelope models to predict the
616 effect of climate change on species distributions. *Global change biology*, 12(12):2272–2281, 2006.
- 617 Robert J Hijmans, Steven Phillips, John Leathwick, Jane Elith, and Maintainer Robert J Hijmans.
618 Package ‘dismo’. *Circles*, 9(1):1–68, 2017.
- 619 Janneke HilleRisLambers, Melanie A Harsch, Ailene K Ettinger, Kevin R Ford, and Elinore J
620 Theobald. How will biotic interactions influence climate change-induced range shifts? *Annals*
621 *of the New York Academy of Sciences*, 1297(1):112–125, 2013.
- 622 IPCC. Climate change 2021: The physical science basis, 2021. URL
623 <https://www.ipcc.ch/report/ar6/wg1/>.
- 624 Nick JB Isaac, Marta A Jarzyna, Petr Keil, Lea I Dambly, Philipp H Boersch-Supan, Ella Browning,
625 Stephen N Freeman, Nick Golding, Gurutzeta Guillera-Arroita, Peter A Henrys, et al. Data

- 626 integration for large-scale models of species distributions. *Trends in ecology & evolution*, 35(1):
627 56–67, 2020.
- 628 Alberto Jiménez-Valverde. Insights into the area under the receiver operating characteristic curve
629 (auc) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeog-*
630 *raphy*, 21(4):498–507, 2012.
- 631 David Kahle, Hadley Wickham, and Maintainer David Kahle. Package ‘ggmap’. *Retrieved Septem-*
632 *ber*, 5:2021, 2019.
- 633 Melanie R Kazenel, Catherine L Debban, Luciana Ranelli, Will Q Hendricks, Y Anny Chung,
634 Thomas H Pendergast IV, Nikki D Charlton, Carolyn A Young, and Jennifer A Rudgers. A
635 mutualistic endophyte alters the niche dimensions of its host plant. *AoB plants*, 7:plv005, 2015.
- 636 Roland A Knapp, Gary M Fellers, Patrick M Kleeman, David AW Miller, Vance T Vredenburg,
637 Erica Bree Rosenblum, and Cheryl J Briggs. Large-scale recovery of an endangered amphibian
638 despite ongoing exposure to multiple stressors. *Proceedings of the National Academy of Sciences*,
639 113(42):11889–11894, 2016.
- 640 Mikhail V Kozlov, Irina V Sokolova, Vitali Zverev, Alexander A Egorov, Mikhail Y Goncharov,
641 and Elena L Zvereva. Biases in estimation of insect herbivory from herbarium specimens.
642 *Scientific Reports*, 10(1):12298, 2020.
- 643 James Lendemer, Barbara Thiers, Anna K Monfils, Jennifer Zaspel, Elizabeth R Ellwood, Andrew
644 Bentley, Katherine LeVan, John Bates, David Jennings, Dori Contreras, et al. The extended
645 specimen network: A strategy to enhance us biodiversity collections, promote research and
646 education. *BioScience*, 70(1):23–30, 2020.
- 647 A Leuchtmann. Systematics, distribution, and host specificity of grass endophytes. *Natural toxins*,
648 1(3):150–162, 1992.
- 649 Adrian Leuchtmann, Charles W Bacon, Christopher L Schardl, James F White Jr, and Mariusz

- 650 Tadych. Nomenclatural realignment of neotyphodium species with genus epichloë. *Mycologia*,
651 106(2):202–215, 2014.
- 652 Finn Lindgren, Håvard Rue, and Johan Lindström. An explicit link between gaussian fields and
653 gaussian markov random fields: the stochastic partial differential equation approach. *Journal*
654 *of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4):423–498, 2011.
- 655 Canran Liu, Pam M Berry, Terence P Dawson, and Richard G Pearson. Selecting thresholds of
656 occurrence in the prediction of species distributions. *Ecography*, 28(3):385–393, 2005.
- 657 Margaret McFall-Ngai, Michael G Hadfield, Thomas CG Bosch, Hannah V Carey, Tomislav
658 Domazet-Lošo, Angela E Douglas, Nicole Dubilier, Gerard Eberl, Tadashi Fukami, Scott F
659 Gilbert, et al. Animals in a bacterial world, a new imperative for the life sciences. *Proceedings*
660 *of the National Academy of Sciences*, 110(9):3229–3236, 2013.
- 661 Timothy D Meehan, Nicole L Michel, and Håvard Rue. Spatial modeling of audubon christmas
662 bird counts reveals fine-scale patterns and drivers of relative abundance trends. *Ecosphere*, 10
663 (4):e02707, 2019.
- 664 Emily K Meineke, Charles C Davis, and T Jonathan Davies. The unrealized potential of herbaria
665 for global change biology. *Ecological Monographs*, 88(4):505–525, 2018.
- 666 Emily K Meineke, Aimée T Classen, Nathan J Sanders, and T Jonathan Davies. Herbarium
667 specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1):105–117,
668 2019.
- 669 Abigail R Meyer, Maria Valentin, Laima Liulevicius, Tami R McDonald, Matthew P Nelsen, Jean
670 Pengra, Robert J Smith, and Daniel Stanton. Climate warming causes photobiont degradation
671 and c starvation in a boreal climate sentinel lichen. *American Journal of Botany*, 2022.
- 672 David AW Miller, Krishna Pacifici, Jamie S Sanderlin, and Brian J Reich. The recent past and

- 673 promising future for data integration methods to estimate species' distributions. *Methods in*
674 *Ecology and Evolution*, 10(1):22–37, 2019.
- 675 Daniel S Park, Ian Breckheimer, Alex C Williams, Edith Law, Aaron M Ellison, and Charles C
676 Davis. Herbarium specimens reveal substantial and unexpected variation in phenological sen-
677 sitivity across the eastern united states. *Philosophical Transactions of the Royal Society B*, 374
678 (1763):20170394, 2019.
- 679 Martin Parniske. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Reviews*
680 *Microbiology*, 6(10):763–775, 2008.
- 681 Anton Pauw and Julie A Hawkins. Reconstruction of historical pollination rates reveals linked
682 declines of pollinators and plants. *Oikos*, 120(3):344–349, 2011.
- 683 Shilong Piao, Qiang Liu, Anping Chen, Ivan A Janssens, Yongshuo Fu, Junhu Dai, Lingli Liu,
684 XU Lian, Miaogen Shen, and Xiaolin Zhu. Plant phenology and global climate change: Current
685 progresses and challenges. *Global change biology*, 25(6):1922–1940, 2019.
- 686 Timothée Poisot, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew Mac-
687 Donald, Benjamin Mercier, Clément Violet, and Steve Vissault. Global knowledge gaps in
688 species interaction networks data. *Journal of Biogeography*, 48(7):1552–1563, 2021.
- 689 Nicole E Rafferty, Paul J CaraDonna, and Judith L Bronstein. Phenological shifts and the fate of
690 mutualisms. *Oikos*, 124(1):14–21, 2015.
- 691 Christopher J Raxworthy and Brian Tilston Smith. Mining museums for historical dna: advances
692 and challenges in museomics. *Trends in Ecology & Evolution*, 36(11):1049–1060, 2021.
- 693 François Renoz, Inès Pons, and Thierry Hance. Evolutionary responses of mutualistic insect–
694 bacterial symbioses in a world of fluctuating temperatures. *Current opinion in insect science*, 35:
695 20–26, 2019.

- 696 Elizabeth Lewis Roberts and Aileen Ferraro. Rhizosphere microbiome selection by epichloë en-
697 dophytes of *festuca arundinacea*. *Plant and soil*, 396:229–239, 2015.
- 698 RJ Rodriguez, JF White Jr, Anne E Arnold, and a RS and Redman. Fungal endophytes: diversity
699 and functional roles. *New phytologist*, 182(2):314–330, 2009.
- 700 Gregor Rolshausen, Francesco Dal Grande, Anna D Sadowska-Deś, Jürgen Otte, and Imke
701 Schmitt. Quantifying the climatic niche of symbiont partners in a lichen symbiosis indicates
702 mutualist-mediated niche expansions. *Ecography*, 41(8):1380–1392, 2018.
- 703 Jennifer A Rudgers and Angela L Swafford. Benefits of a fungal endophyte in *elymus virginicus*
704 decline under drought stress. *Basic and Applied Ecology*, 10(1):43–51, 2009.
- 705 Jennifer A Rudgers, Michelle E Afkhami, Megan A Rúa, Andrew J Davitt, Samantha Hammer,
706 and Valérie M Huguet. A fungus among us: broad patterns of endophyte distribution in the
707 grasses. *Ecology*, 90(6):1531–1539, 2009.
- 708 Jennifer A Rudgers, Rebecca A Fletcher, Eric Olivas, Carolyn A Young, Nikki D Charlton, Dean E
709 Pearson, and John L Maron. Long-term ungulate exclusion reduces fungal symbiont prevalence
710 in native grasslands. *Oecologia*, 181:1151–1161, 2016.
- 711 Håvard Rue, Sara Martino, and Nicolas Chopin. Approximate bayesian inference for latent gaus-
712 sian models by using integrated nested laplace approximations. *Journal of the royal statistical
713 society: Series b (statistical methodology)*, 71(2):319–392, 2009.
- 714 Kari Saikkonen, Pedro E Gundel, and Marjo Helander. Chemical ecology mediated by fungal
715 endophytes in grasses. *Journal of chemical ecology*, 39:962–968, 2013.
- 716 Michelle E Sneck, Jennifer A Rudgers, Carolyn A Young, and Tom EX Miller. Variation in the
717 prevalence and transmission of heritable symbionts across host populations in heterogeneous
718 environments. *Microbial Ecology*, 74:640–653, 2017.

- 719 Thomas F Stocker, Dahe Qin, G-K Plattner, Lisa V Alexander, Simon K Allen, Nathaniel L Bindoff,
720 F-M Bréon, John A Church, Ulrich Cubasch, Seita Emori, et al. Technical summary. In *Climate*
721 *change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment*
722 *Report of the Intergovernmental Panel on Climate Change*, pages 33–115. Cambridge University
723 Press, 2013.
- 724 Peter A Stott, Nathan P Gillett, Gabriele C Hegerl, David J Karoly, Dáithí A Stone, Xuebin Zhang,
725 and Francis Zwiers. Detection and attribution of climate change: a regional perspective. *Wiley*
726 *interdisciplinary reviews: climate change*, 1(2):192–211, 2010.
- 727 S Sully, DE Burkepile, MK Donovan, G Hodgson, and R Van Woesik. A global analysis of coral
728 bleaching over the past two decades. *Nature communications*, 10(1):1–5, 2019.
- 729 E Toby Kiers, Todd M Palmer, Anthony R Ives, John F Bruno, and Judith L Bronstein. Mutualisms
730 in a changing world: an evolutionary perspective. *Ecology letters*, 13(12):1459–1474, 2010.
- 731 Andrew T Tredennick, Giles Hooker, Stephen P Ellner, and Peter B Adler. A practical guide to
732 selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102(6):e03336,
733 2021.
- 734 Amy M Truitt, Martin Kapun, Rupinder Kaur, and Wolfgang J Miller. Wolbachia modifies thermal
735 preference in drosophila melanogaster. *Environmental microbiology*, 21(9):3259–3268, 2019.
- 736 Shripad D. Tuljapurkar. Population dynamics in variable environments. III. Evo-
737 lutionary dynamics of r-selection. *Theoretical Population Biology*, 21(1):141–165,
738 February 1982. ISSN 0040-5809. doi: 10.1016/0040-5809(82)90010-7. URL
739 <http://www.sciencedirect.com/science/article/pii/0040580982900107>.
- 740 Veronika Vikuk, Carolyn A Young, Stephen T Lee, Padmaja Nagabhyru, Markus Krischke, Mar-
741 tin J Mueller, and Jochen Krauss. Infection rates and alkaloid patterns of different grass species
742 with systemic epichloë endophytes. *Applied and Environmental Microbiology*, 85(17):e00465–19,
743 2019.

- 744 Zhengfeng Wang, Chunjie Li, and James White. Effects of epichloë endophyte infection on
745 growth, physiological properties and seed germination of wild barley under saline conditions.
746 *Journal of Agronomy and Crop Science*, 206(1):43–51, 2020.
- 747 Robert J Warren and Mark A Bradford. Mutualism fails when climate response differs between
748 interacting species. *Global Change Biology*, 20(2):466–474, 2014.
- 749 Nicole S Webster, Rose E Cobb, and Andrew P Negri. Temperature thresholds for bacterial
750 symbiosis with a sponge. *The ISME journal*, 2(8):830–842, 2008.
- 751 James F White and Garry T Cole. Endophyte-host associations in forage grasses. i. distribution
752 of fungal endophytes in some species of lolium and festuca. *Mycologia*, 77(2):323–327, 1985.
- 753 Franziska M Willems, JF Scheepens, and Oliver Bossdorf. Forest wildflowers bloom earlier as
754 europe warms: lessons from herbaria and spatial modelling. *New Phytologist*, 235(1):52–65,
755 2022.
- 756 Charles G Willis, Elizabeth R Ellwood, Richard B Primack, Charles C Davis, Katelin D Pearson,
757 Amanda S Gallinat, Jenn M Yost, Gil Nelson, Susan J Mazer, Natalie L Rossington, et al. Old
758 plants, new tricks: Phenological research using herbarium specimens. *Trends in ecology &*
759 *evolution*, 32(7):531–546, 2017.
- 760 Chao Xia, Nana Li, Yawen Zhang, Chunjie Li, Xingxu Zhang, and Zhibiao Nan. Role of epichloë
761 endophytes in defense responses of cool-season grasses to pathogens: A review. *Plant disease*,
762 102(11):2061–2073, 2018.
- 763 Kentaro Yoshida, Eriko Sasaki, and Sophien Kamoun. Computational analyses of ancient
764 pathogen dna from herbarium samples: challenges and prospects. *Frontiers in plant science*,
765 6:771, 2015.