

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

13 Species' distributions and abundances are shifting in response to climate change. Most species
14 harbor microbial symbionts that have the potential to influence these responses. Mutualistic
15 microbial symbionts may provide resilience to environmental change by protecting their hosts
16 from increasing stress. However, environmental change that disrupts these interactions may
17 lead to declines in hosts or symbionts. Microbes preserved within herbarium specimens offer a
18 unique opportunity to quantify changes in microbial symbiosis across broad temporal and spatial
19 scales. We asked how the prevalence of seed-transmitted fungal symbionts of grasses (*Epichloë*
20 endophytes), which can protect hosts from abiotic stress, have changed over time in response to
21 climate change, and how these changes vary across host species' ranges. Specifically, we analyzed
22 2,346 herbarium specimens of three grass host species collected over the last two centuries (1824
23 – 2019) for the presence or absence of endophyte symbiosis, and evaluated spatial and temporal
24 trends in endophyte prevalence. We found that endophytes have increased in prevalence over
25 the last two centuries from ca. 25% prevalence to ca. 75% prevalence, on average, across the
26 three host species. We also found that changes in prevalence were associated with observed
27 changes in seasonal climate drivers² corresponding to each host species' peak growing season.
28 Our analysis performed favorably in an out-of-sample predictive test, however we identified
29 XXX as suggesting the model fusion may be an important step moving forward. Our results
30 provide novel evidence for a cryptic biological response to climate change that may contribute to
31 the resilience of host-microbe symbiosis through context-dependent benefits that confer a fitness
32 advantage to symbiotic hosts under environmental change.³

²Describe "changes" – warming? drying?

³I like this and the abstract in general. I agree with Tom and I think we have some space to add these details. Abstract : 300

Introduction

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

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

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

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

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

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

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

99 Early research on *Epichloë* used herbarium specimens to describe the broad taxonomic di-
100 versity of host species that harbor these symbionts (White and Cole, 1985), establishing that
101 endophyte symbiosis could be identified in plant tissue from as early as 1851.⁴ However, no
102 subsequent studies, to our knowledge, have used the vast resources of biological collections to
103 quantitatively assess spatio-temporal trends in endophyte prevalence and their environmental
104 correlates. Grasses are commonly collected and identified based on the presence of their re-
105 productive structures, meaning that preserved specimens typically contain seeds, conveniently
106 preserving the fungi along with their host plants on herbarium sheets. This creates the oppor-
107 tunity to leverage the unique spatio-temporal sampling of herbarium collections to examine the
108 response of the symbiosis to historical climate change. Research using historical collections has
109 clearly demonstrated other ecological signatures of a changing climate. However the predictive
110 ability of these historical analyses is rarely tested against contemporary data (Lee et al., 2024).
111 Identifying the ways in which these analyses fall short is a crucial step for the field move from

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

112 reading signatures in the past to forecasting ecological dynamics into the future.⁵

113 In this study, we assessed the long-term responses of endophyte symbiosis to climate change
114 through the use of herbarium specimens of three North American host grass species (*Agrostis*
115 *hyemalis*, *Agrostis perennans*, and *Elymus virginicus*). We first address questions describing spatial
116 and temporal trends in endophyte prevalence: (i) How has endophyte prevalence changed over
117 the past two centuries? and (ii) How spatially variable are temporal trends in endophyte preva-
118 lence across eastern North America? We then address how climate change may be driving trends
119 in endophyte prevalence by asking: (iii) What is the relationship between variation in temporal
120 trends in endophyte prevalence and changes in climate drivers? We predicted that aggregate en-
121 dophyte prevalence would increase over time in tandem with climate warming, and that hotspots
122 of endophyte change would correspond spatially to hotspots of climate change. Finally, we eval-
123 uated the performance of models built on data from historic specimens with an out-of-sample
124 test, data on endophyte prevalence from contemporary surveys of host populations. To answer
125 these questions we examined a total of 2,346 specimens collected across eastern North America
126 between 1824 and 2019.⁶

127

Methods

128

Focal species

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

5what do you think of this? trying to presage the out-of-sample test without over promising and without saying outright that our analysis sucks. Is this the right place for this? I had imagined some of this material will be really developed in the discussion.

6I think the consensus was to keep the out-of-sample validation which should absolutely go into the Intro as an important element of novelty. Should go in the Abstract too.

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

¹⁴⁴ *Herbarium surveys*

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

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

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

¹⁸² *Modeling spatial and temporal changes in endophyte prevalence*

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

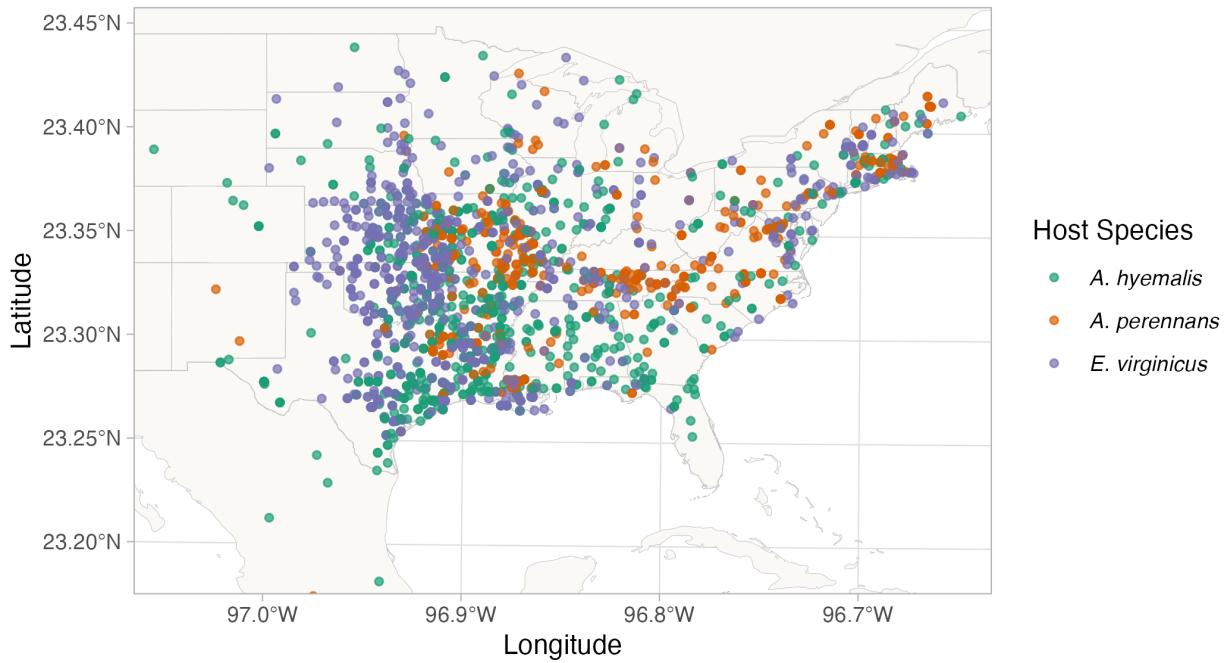


Figure 1: Collection locations of herbarium specimens of three grass host species across eastern North America that were sampled for *Epichloë* endophyte presence or absence.

across the spatial extent of each host's distribution. To appropriately account for the spatial non-independence of geo-referenced occurrences⁷, we used an approximate Bayesian method, Integrated Nested Laplace Approximation (INLA), to construct spatio-temporal models of endophyte prevalence. INLA provides a computationally efficient method of ascertaining parameter posterior distributions for certain models that can be formulated as latent Gaussian Models (Rue et al., 2009). Many common statistical models, including structured and unstructured mixed-effects models, can be represented as latent Gaussian Models. We incorporated spatial heterogeneity into this analysis using spatially-structured intercept and slope parameters implemented as stochastic partial differential equation (SPDE) approximations of a continuous spatial Gaussian process. This SPDE approach is a flexible method of smoothing across space while explicitly accounting for spatial dependence between data-points (Bakka et al., 2018; Lindgren

⁷ spelling?

¹⁹⁷ et al., 2011). Fitting models with structured spatial effects is possible with MCMC sampling but
¹⁹⁸ can require long computation times, making INLA an effective alternative, which has been used
¹⁹⁹ to model spatial patterns in flowering phenology (Willems et al., 2022), the abundance of bird
²⁰⁰ species (Meehan et al., 2019) and butterflies (Crossley et al., 2022), the distribution of temperate
²⁰¹ trees (Engel et al., 2022) as well as the population dynamics of endangered amphibians (Knapp
²⁰² et al., 2016) and other ecological processes (Beguin et al., 2012).

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

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

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

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

$$(1d)$$

²¹⁴ Previous work suggests that behavior of historical botanists and uneven sampling may intro-
²¹⁵ duce biases into ecological inferences made from historic collections (Kozlov et al., 2020). Prolific
²¹⁶ collectors who contribute thousands of specimens may be more or less likely to collect certain
²¹⁷ species, or specimens with certain traits (Daru et al., 2018). Similarly, the process of scoring seeds

218 for hyphae involved several student researchers who, even with standardized training, may vary
219 in their likelihood of positively identifying *Epichloë* hyphae. By including a random effect for
220 collectors and for scorers, we attempted to account for variance across individual researchers
221 that may bias our predictions of changes in endophyte prevalence.

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

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

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

8

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

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

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

²⁵⁵ *Assessing the role of climate drivers*

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

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

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

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

286 15

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

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

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

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

287

Modeling distributions of host species

288 We modeled the distribution of each host species to generate maps on which we predicted the
 289 dynamics of *Epichloë* symbionts. We followed the ODMAP (overview, data, model, assessment,
 290 prediction) protocol (Crossley et al., 2022), using presence-only observations of the host species
 291 from GBIF between 1990 to 2020¹⁶. To reduce the potential influence of sampling bias and spa-
 292 tial autocorrelation, we thinned the occurrences to the spatial scale ()¹⁷ of our selected climatic
 293 predictors. We selected climate variables that aligned with our analysis of climatic influences on
 294 trends in endophyte prevalence described above. We calculated the mean and standard deviation
 295 of seasonal temperature and precipitation across 1990 to 2020. Among this suite of variables,
 296 we chose to include mean spring temperature, mean spring precipitation, and mean summer
 297 temperature¹⁸, which were uncorrelated (Variance Inflation Factor > 0.7) and allowed us to pre-
 298 dict the occurrence probability of each host species in space and time. We fit maximum entropy
 299 (MaxEnt) models using the maxent function in the package dismo (Hijmans et al., 2017). Max-
 300 Ent is preferred because it has been shown to generate response curves with less unpredictable
 301 behavior when applied to new climates (Hijmans and Graham, 2006).¹⁹ We generated 10,000
 302 pseudo-absences as background points, and split the occurrence data into 75% for model train-
 303 ing and 25% for model testing. The performance of models was evaluated with AUC AUC²⁰
 304 (Jiménez-Valverde, 2012). To convert the continuous predicted probabilities into binary presence
 305 - absence maps, we used the training sensitivity (true positive rate) and specificity threshold
 306 (true negative rate) (Liu et al., 2005). These binary maps serve as boundaries in presented maps
 307 of change in endophyte prevalence, and outline the set of pixels used in our analysis of climate

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.

¹⁶How many data points does this end up being?

¹⁷I think this is 4km, but need to check

¹⁸is this list accurate? my re-running my climate analysis means we ought to re-run the sdm's, and use SD instead of CV, so we can update this list based on whatever is appropriate

¹⁹possibly could remove this sentence?

²⁰can we add these values?

³⁰⁸ correlates with trends in endophyte prevalence

³⁰⁹ **Results**

³¹⁰ *How has endophyte prevalence changed over time?*

³¹¹ We found that endophyte prevalence increased within the examined specimens over the last two
³¹² centuries for all three host species (Fig. 2). On average, modeling indicated that endophytes of *A.*
³¹³ *perennans* and *E. virginicus* increased from ~ 40 % to 70% prevalence across the study region, and
³¹⁴ that of *A. hyemalis* increased from ~ 25% to over 50% prevalence. Our model indicates a high
³¹⁵ certainty that overall temporal trends are positive across species (99% probability of a positive
³¹⁶ overall year slope in *A. hyemalis*, 92% probability of a positive overall year slope in *A. perennans*,
³¹⁷ and 91% probability of a positive overall year slope in *E. virginicus*) (Fig. A6)

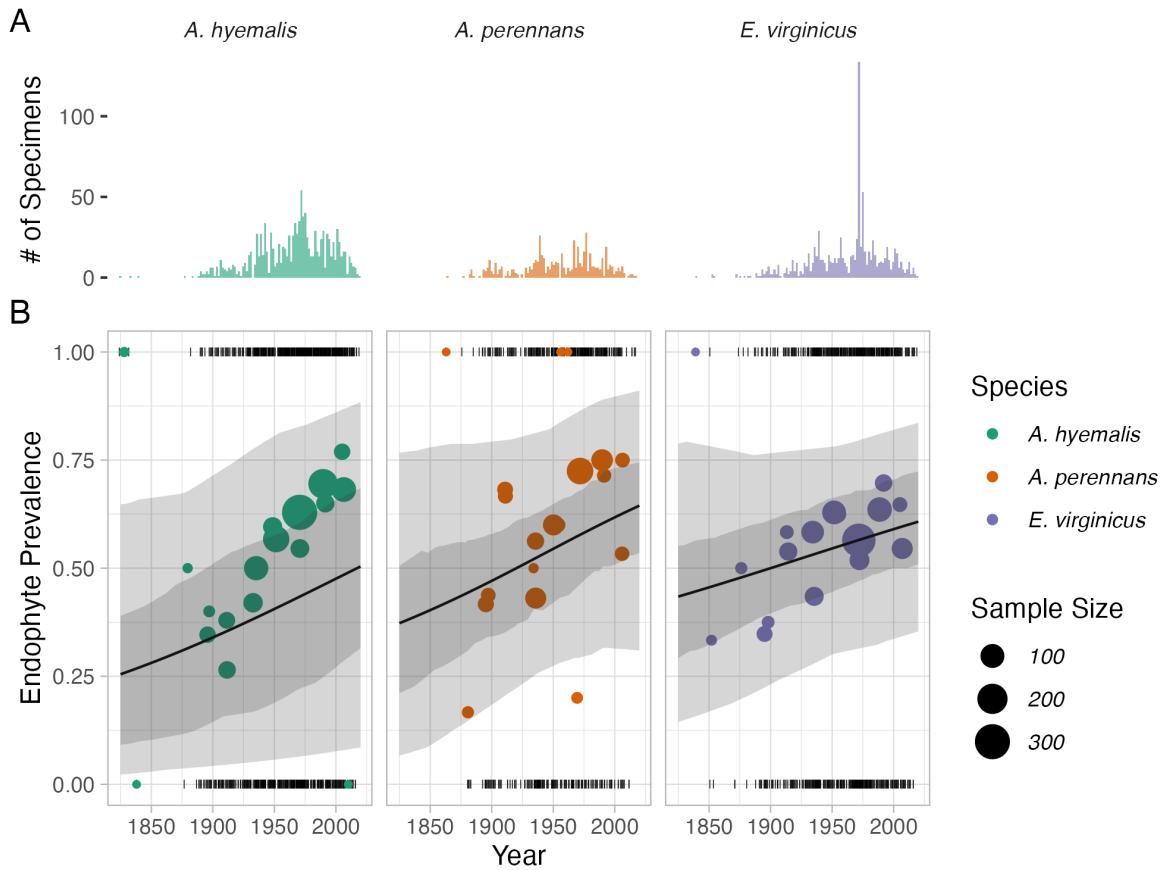


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of scored specimens through time for each host species. (B) Lines show predicted mean endophyte prevalence over the study period along with the 50% and 95% CI bands incorporating uncertainty associated with collector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

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

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

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

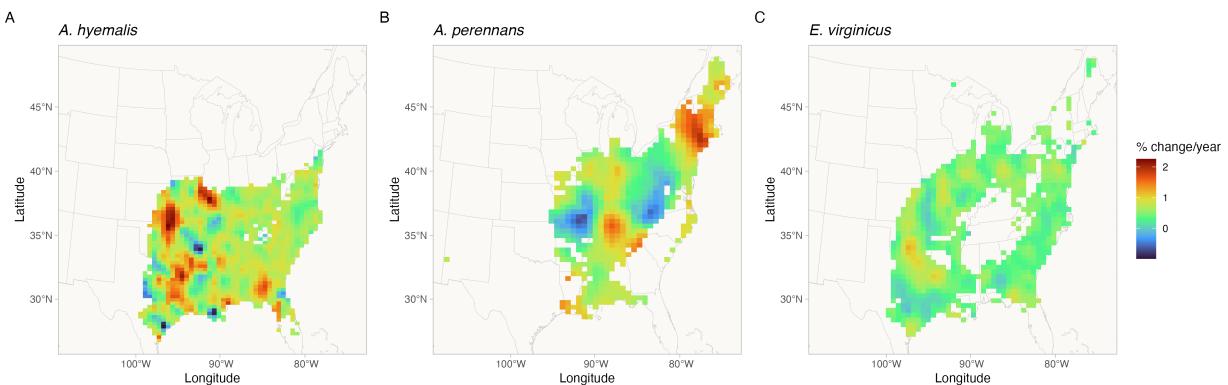


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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

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

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

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

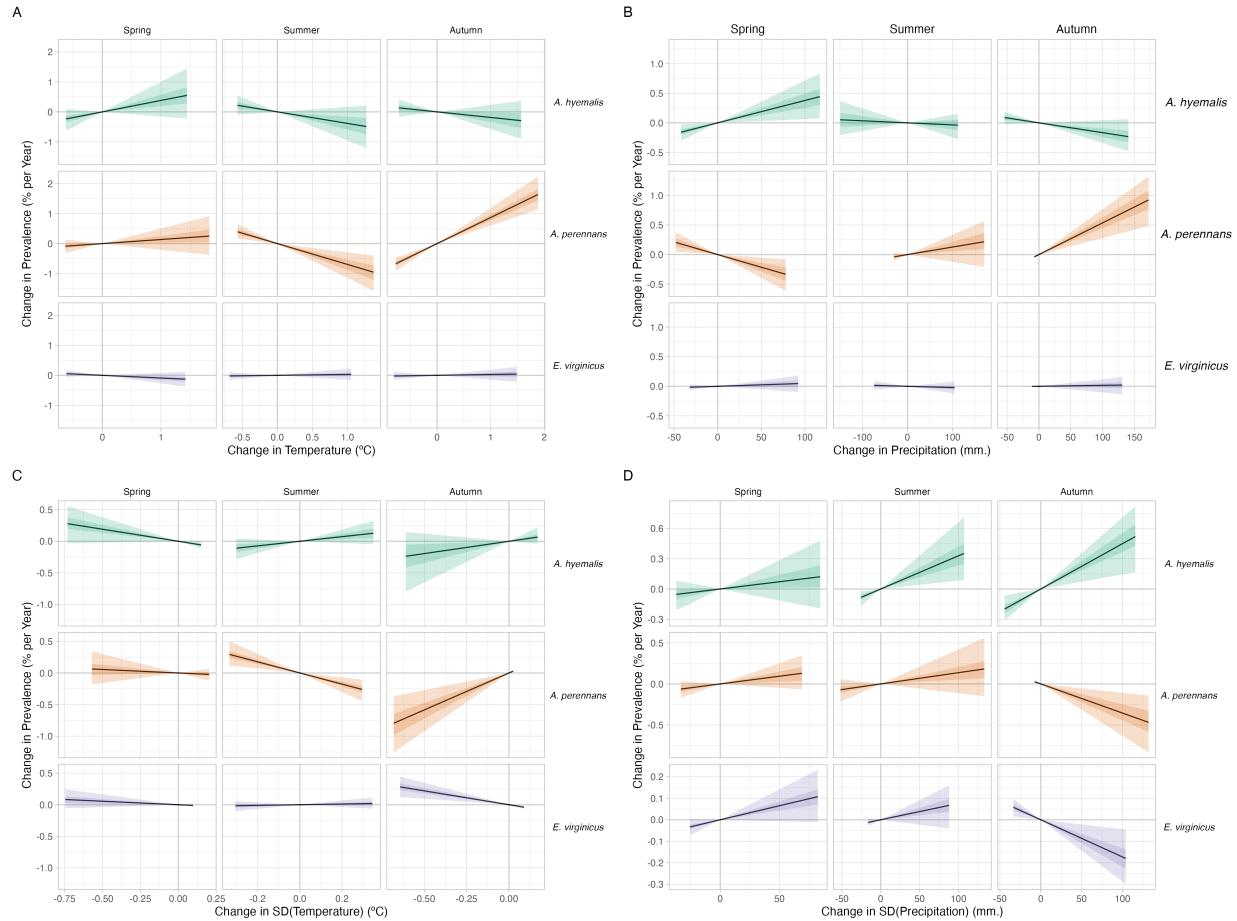


Figure 4: Relationships between changes in seasonal climate drivers and predicted marginal trends in endophyte prevalence. Lines show relationships between seasonal climate (A: mean temperature, B: cumulative precipitation, C: standard deviation in temperature, D: standard deviation in precipitation)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

353 *Performance on test data*

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

³⁵⁸ prevalence towards western longitudes in *A. hyemalis* (Fig. 5A). However, the contemporary
³⁵⁹ data contains additional variability at smaller scales not captured by our sampling of herbarium
³⁶⁰ specimens. We interpreted this to mean that the model captured regional spatial dynamics, but
³⁶¹ underpredicts local scale dynamics. We discuss potential model improvements in the Discussion.

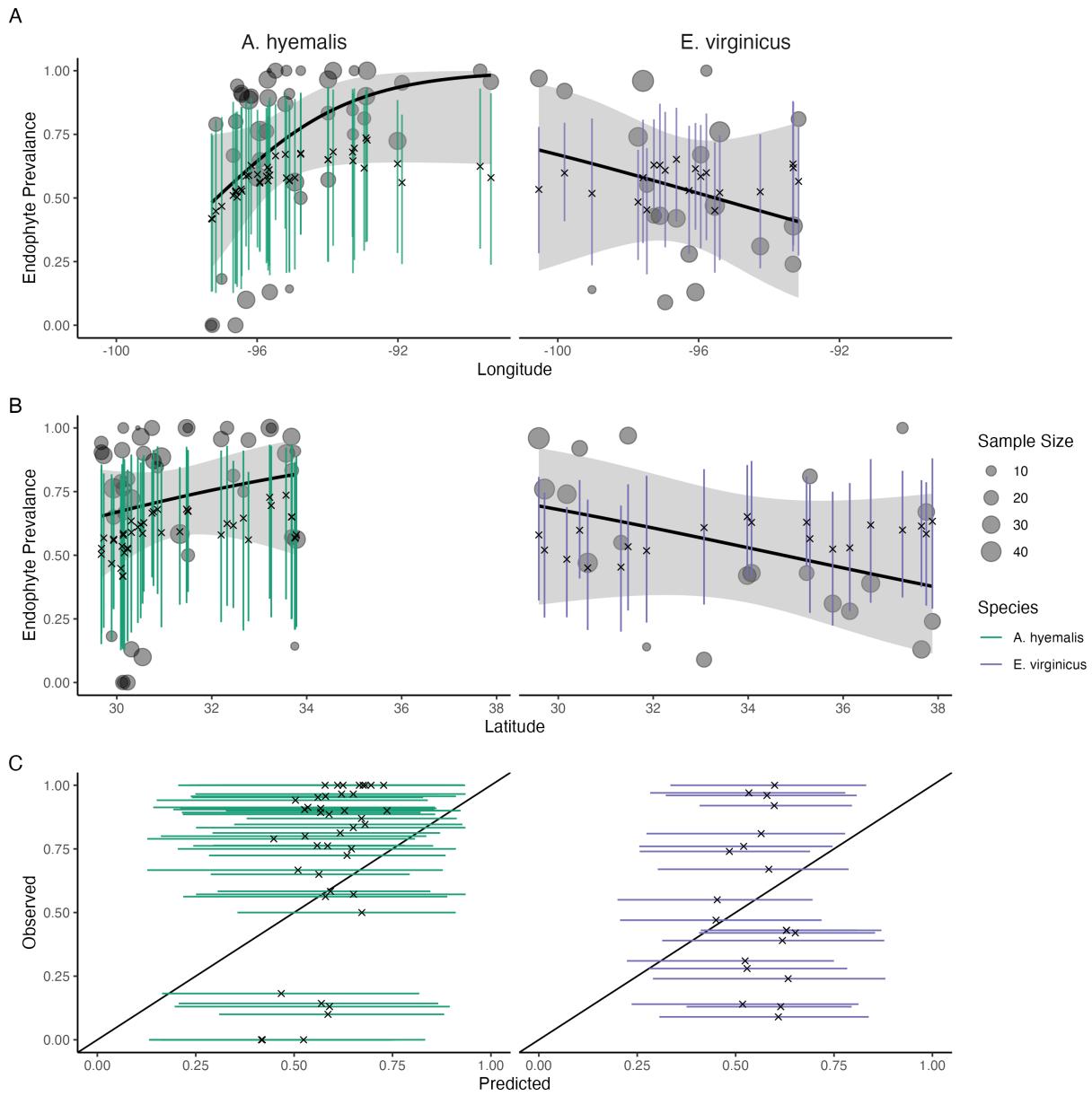


Figure 5: Predicted vs observed endophyte prevalence for contemporary test data. (A) The model, trained on historic herbarium collection data, performed modestly at predicting contemporary endophyte prevalence in *A. hyemalis*, as indicated by some overlap of predicted 95% CI with the 1:1 line, however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

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

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

376 **Discussion**

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

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

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

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

⁴⁴¹ bridge gaps that often exist between large but broad bioclimatic and biodiversity data and small
⁴⁴² but local data on biotic interactions, and move towards the goal of predicting the dynamics of
⁴⁴³ microbial symbioses under climate change (Isaac et al., 2020; Miller et al., 2019).

⁴⁴⁴ Our analysis advances the use of herbarium specimens in global change biology in two ways.
⁴⁴⁵ First and foremost, this is the first study to link long-term changes in microbial symbioses to
⁴⁴⁶ changes in climate using specimens from natural history collections. The responses of micro-
⁴⁴⁷ bial symbioses are a rich target for future studies within museum specimens, particularly those
⁴⁴⁸ that take advantage of advances in sequencing technology. While we used relatively coarse
⁴⁴⁹ presence/absence data based on fungal morphology, other studies have examined historic plant
⁴⁵⁰ microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these
⁴⁵¹ studies have so far been limited to relatively few specimens at limited spatial extents (Bieker
⁴⁵² et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al.,
⁴⁵³ 2015). Continued advances in capturing historic DNA and in filtering out potential contami-
⁴⁵⁴ nation during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith,
⁴⁵⁵ 2021) will be imperative in the effort to scale up these efforts. This scaling up will be essential
⁴⁵⁶ to be able to quantify changes not just in the prevalence of symbionts, but also in symbionts'
⁴⁵⁷ intraspecific variation and evolutionary responses to climate change, as well as in changes in the
⁴⁵⁸ wider microbial community. Answering these questions as well as the unknown questions that
⁴⁵⁹ future researchers may ask also reiterates the value in capturing meta-information during ongo-
⁴⁶⁰ ing digitization efforts at herbaria around the world and during the accession of newly collected
⁴⁶¹ specimens (Edwards et al.; Lendemer et al., 2020). Second, we accounted for several potential
⁴⁶² biases in the data observation process that may be common to many collections-based research
⁴⁶³ questions by using a spatially-explicit random effects model. Spatial autocorrelation (Willems
⁴⁶⁴ et al., 2022), potential biases introduced by the sampling habits of collectors (Daru et al., 2018),
⁴⁶⁵ and variation between contemporary researchers during the collection of trait data, if not cor-
⁴⁶⁶ rected for could lead to over-confident inference about the strength and direction of historic
⁴⁶⁷ change. Previous studies that have quantified the effects of collector biases typically find them

⁴⁶⁸ to be small (Davis et al., 2015; Meineke et al., 2019), and we similarly did not find that collector
⁴⁶⁹ has a strong effect on the results of our analysis.

⁴⁷⁰ Ultimately, a central goal of global change biology is to generate predictive insights into the
⁴⁷¹ future of natural systems. While this survey of historic endophyte prevalence is necessarily cor-
⁴⁷² relative, it serves as a foundation to develop better predictive models of the response of microbial
⁴⁷³ symbioses to climate change. Combining the insights from this type of regional-scale survey with
⁴⁷⁴ field experiments and physiological data could be invaluable. While we found that climate is
⁴⁷⁵ strongly correlated with endophytes' temporal responses, we do not know why trends in preva-
⁴⁷⁶ lence were weak in some areas or how endophytes would respond to more extreme changes in
⁴⁷⁷ climate. For example, transplanting symbiotic and non-symbiotic plants beyond the range edge
⁴⁷⁸ of *A. hyemalis* could tell us whether persistent low endophyte prevalence in that area is a result of
⁴⁷⁹ environmental conditions that lead the symbiosis to negative fitness consequences, or is a result
⁴⁸⁰ of some historical contingency or dispersal limitation that has thus far limited the presence of
⁴⁸¹ symbiotic hosts from a region where they would otherwise flourish and provide resilience. While
⁴⁸² we observed evidence of mutualism resilience, more extreme environmental changes than those
⁴⁸³ observed in our study could potentially push one or both partners beyond their physiological
⁴⁸⁴ limit, leading to the collapse of the mutualism. Our analysis thus far is agnostic to changes in the
⁴⁸⁵ distributions of hosts. Mechanistic models could connect the responses of both host and sym-
⁴⁸⁶ bionts to abiotic climate drivers integrating dispersal processes. Beyond host-microbe symbioses,
⁴⁸⁷ building these types of models would work towards quantitatively attributing biotic responses
⁴⁸⁸ to anthropogenically driven climate change, similar to methods in climate science and economics
⁴⁸⁹ (Carleton and Hsiang, 2016; Stott et al., 2010).

⁴⁹⁰ **Acknowledgments**

⁴⁹¹ We thank Jessica Budke for help in drafting our initial destructive sampling plan, and to the
⁴⁹² many members of herbarium staff who facilitated our research visits, as well as to the hundreds

493 of collectors who contributed to the natural history collections. Several high schooler and un-
494 dergraduate researchers contributed to data collection, including A. Appio-Riley, P. Bilderback,
495 E. Chong, K. Dickens, L. Dufresne, B. Gutierrez, A. Johnson, S. Linder, E. Scales, B. Scherick,
496 K. Schrader, E. Segal , G. Singla, and M. Tucker. This research was supported by funding from
497 National Science Foundation (grants 1754468 and 2208857) and by funding from the Texas Ecolab
498 Program.

499 **Statement of Authorship**

500 J.C.F. contributed to research conception, data collection, data analysis, and led manuscript draft-
501 ing. J.M. contributed to data analysis and manuscript manuscript revisions. T.E.X.M. contributed
502 to research conception, data collection, data analysis, and manuscript revisions.

503 **Data and Code Availability**

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

Appendix A

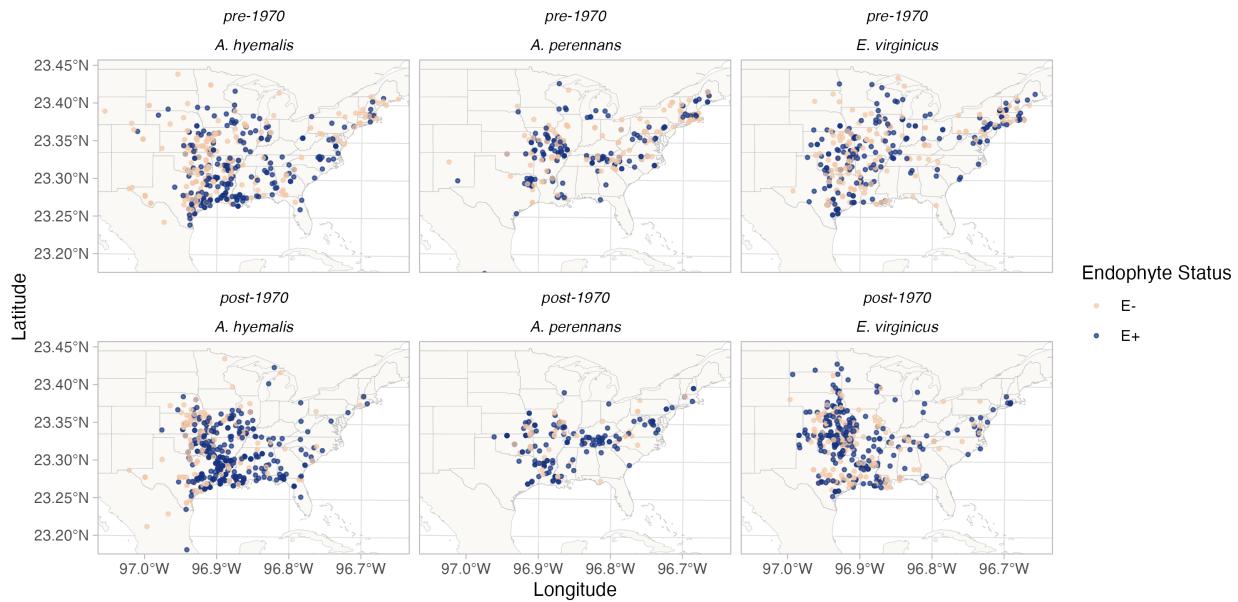


Figure A1: Endophyte presence/absence in specimens of each host species. Points show collection locations colored according to whether the specimen contained endophytes (E+; blue points) or did not contain endophytes (E-, tan points) and are faceted based on collection period.

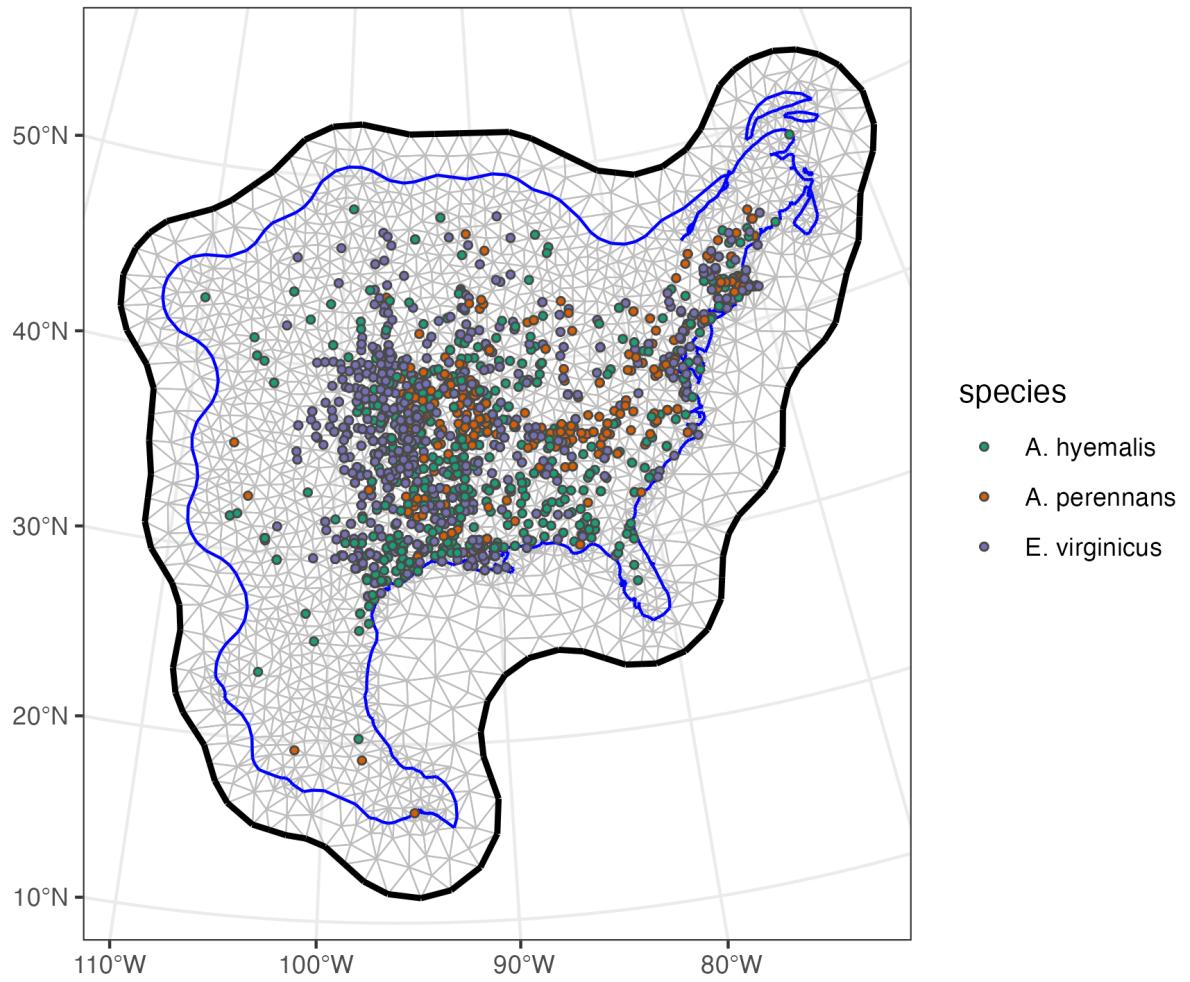


Figure A2: Triangulation mesh used to estimate spatial dependence between data points. Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull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

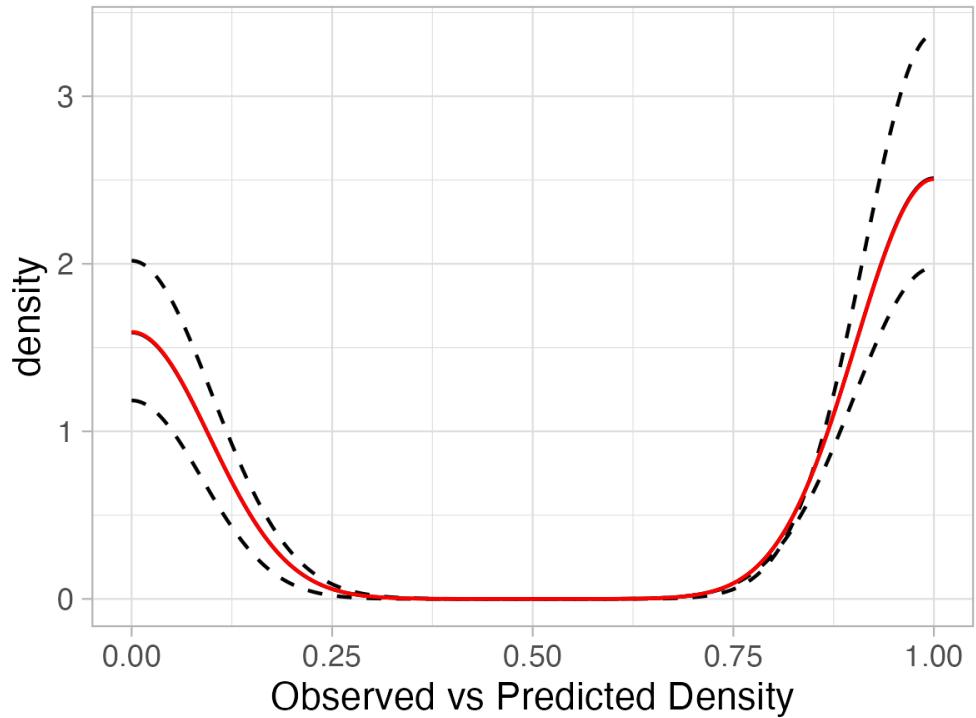


Figure A3: Consistency between real data and simulated values indicate that the fitted model accurately describes the data. Graph shows density curves for the observed data (red) along with the mean(solid) and 95% CI (dashed) of simulated values (black).

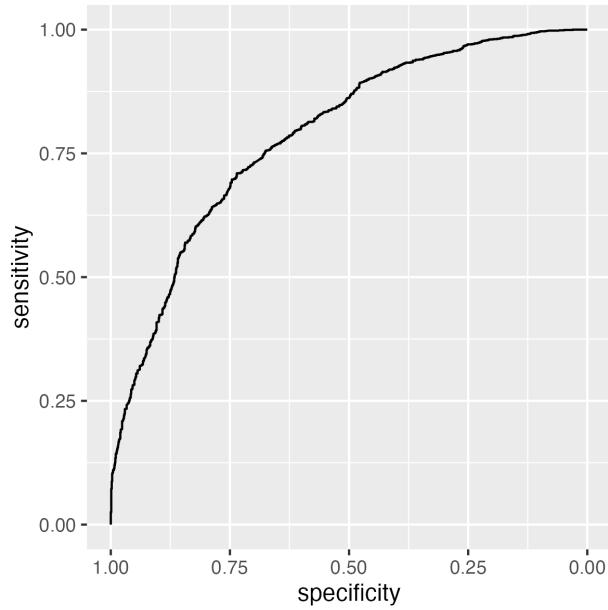


Figure A4: ROC plot showing model performance classifying observations according to endophyte status within the in-sample data. The curves show adequate model performance for observed data. The AUC value is 0.79.

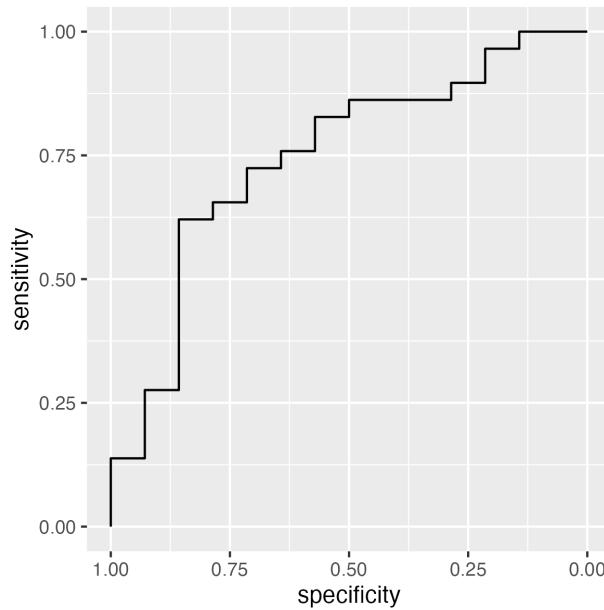


Figure A5: ROC plot showing model performance classifying observations according to endophyte status within the out-of-sample data. The curves show adequate model performance for test data. The AUC value is 0.77.

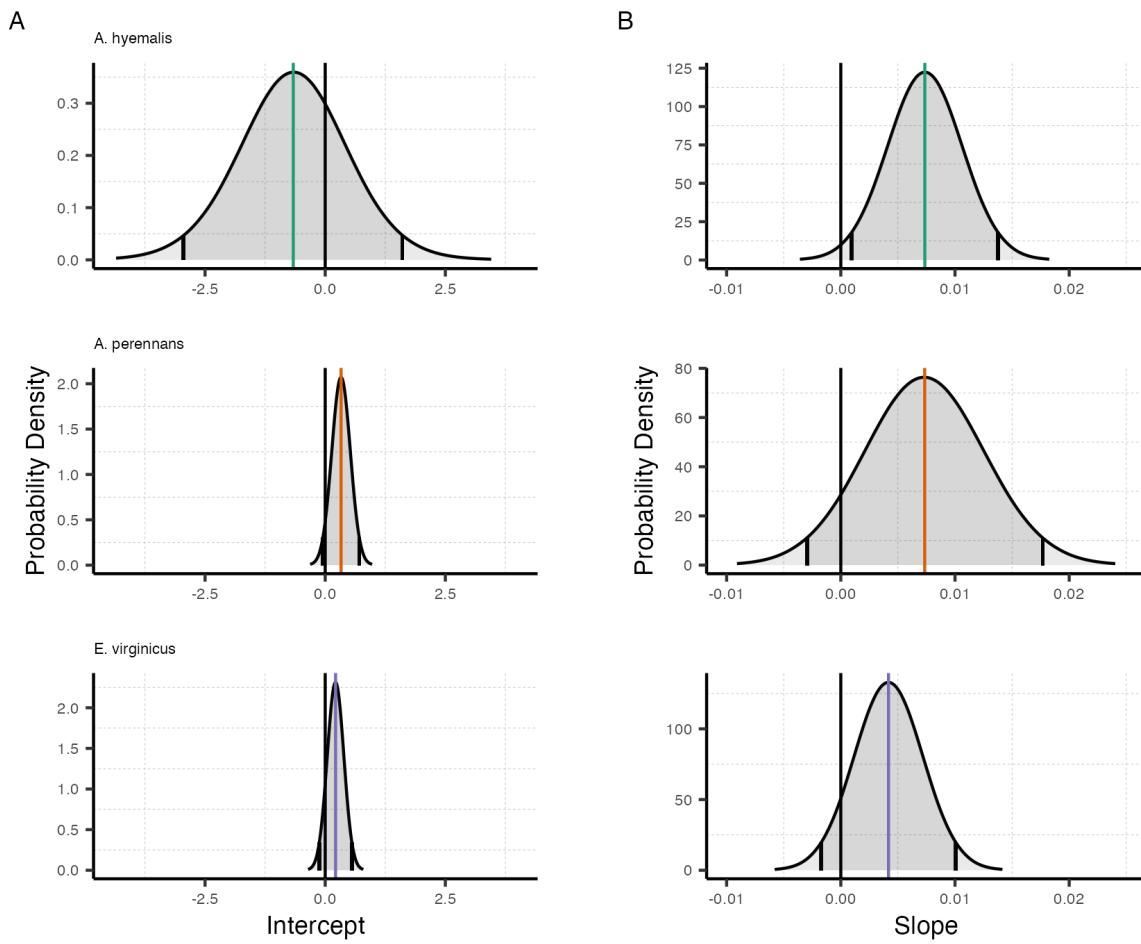


Figure A6: Density curves show the probability density along with mean (colored line) and 95% CI (black lines) for the (A) intercept and (B) slope terms, **A** and **T** respectively. Colors represent each host species

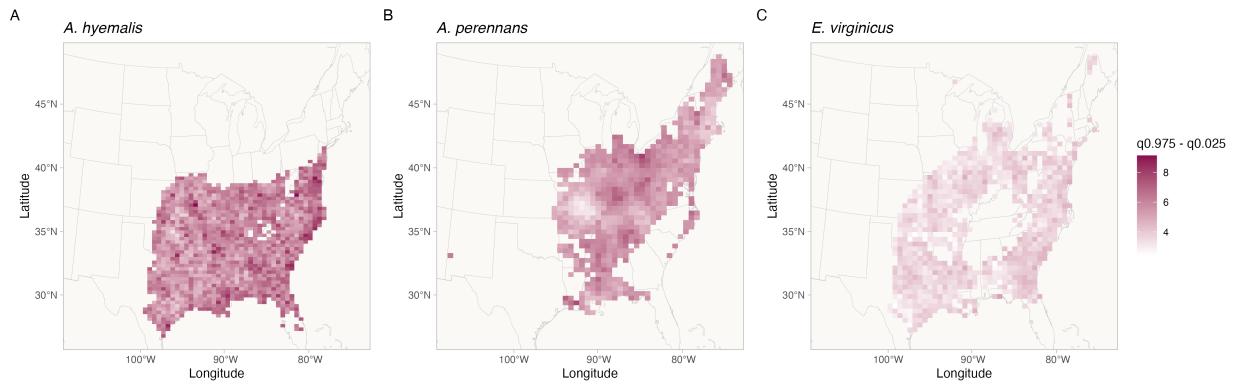


Figure A7: Shading represents the range of the 95% posterior credible interval for spatially varying slopes, τ .

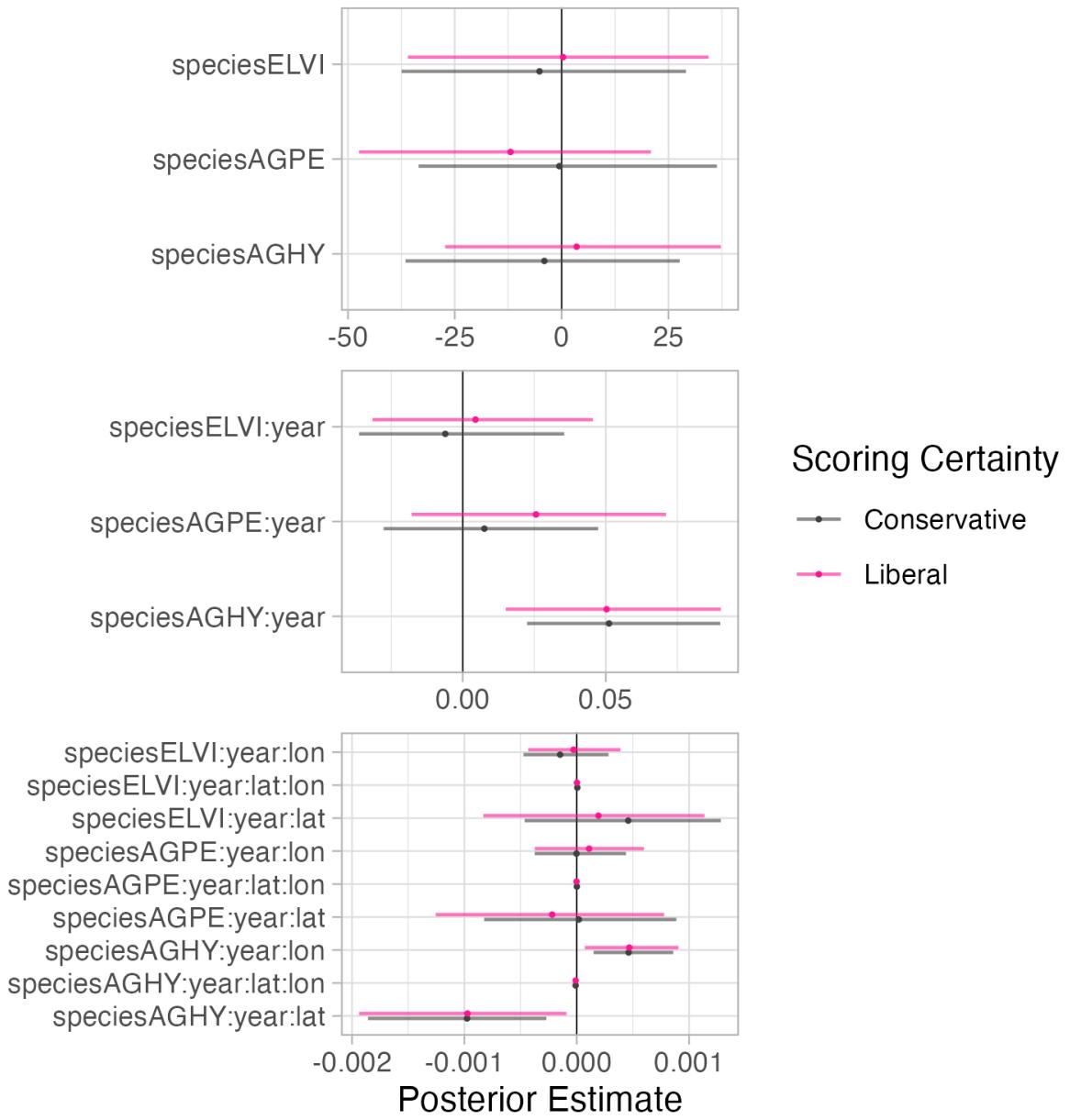


Figure A8: Comparison of posterior estimates of fixed effects when using Liberal or Conservative endophyte scores.

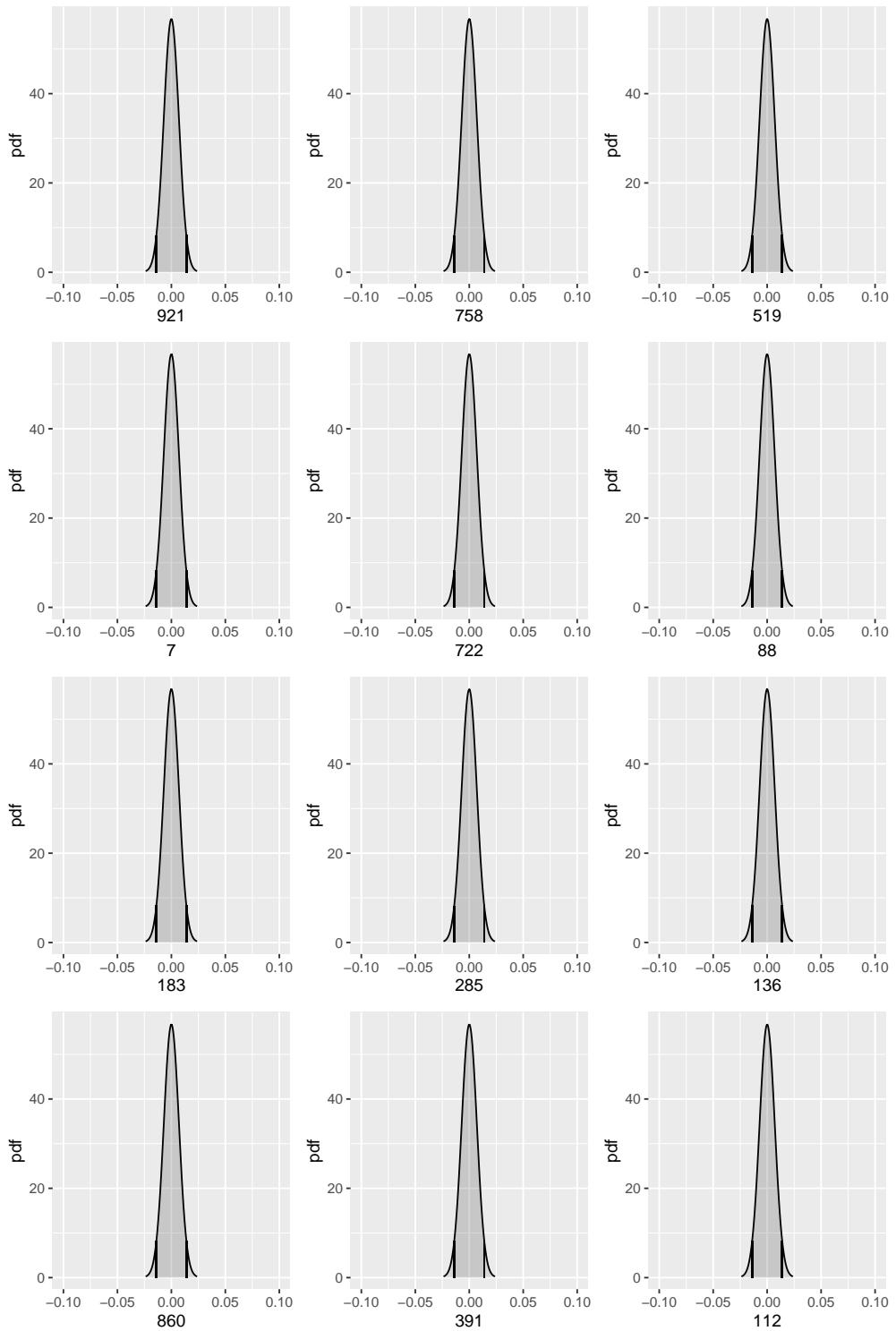


Figure A9: Posterior estimates of collector random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 12 randomly selected collectors.

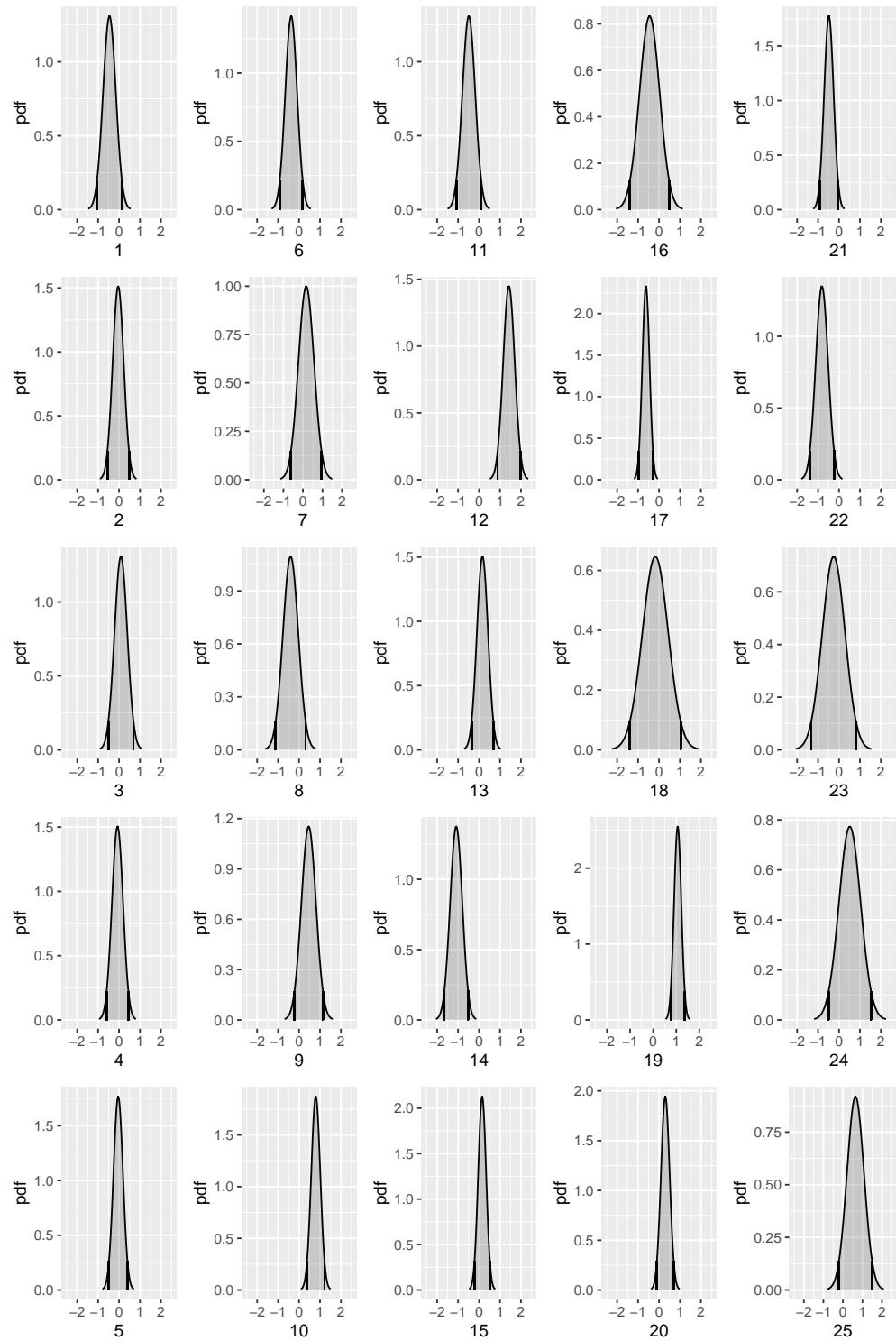


Figure A10: Posterior estimates of scorer random effects. Density curves show the posterior estimate along lines indicating the 95% CI for 25 scorers.

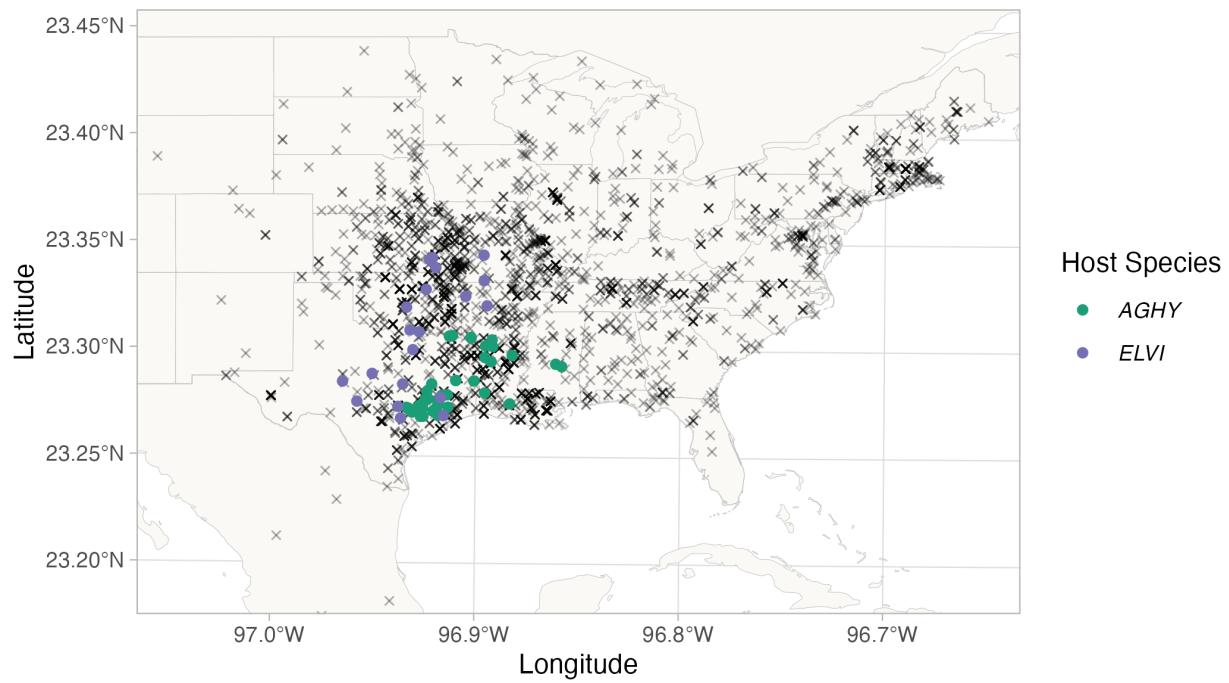
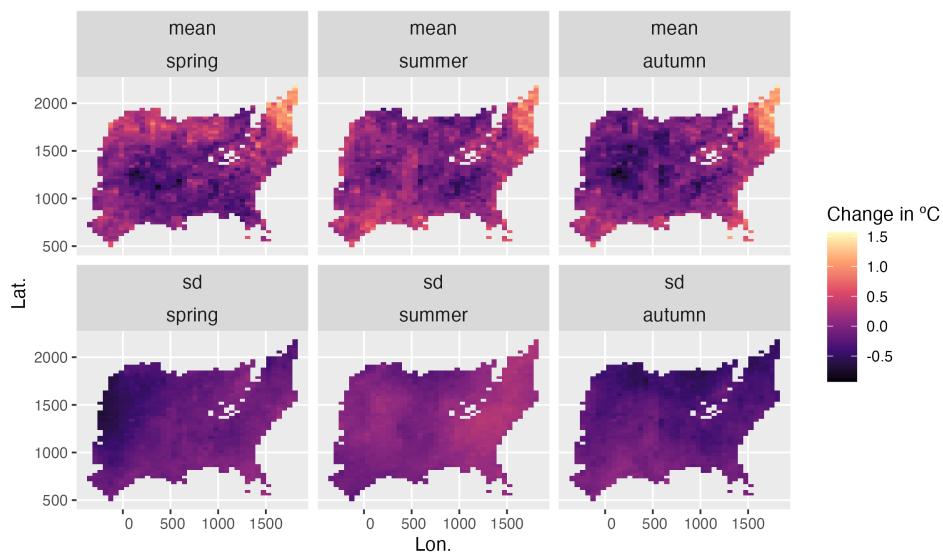


Figure A11: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).

A



B

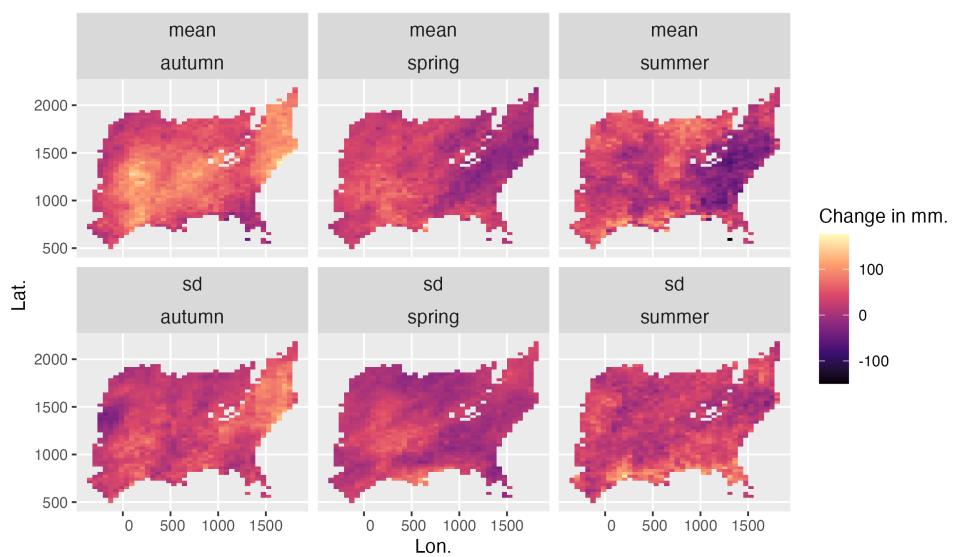
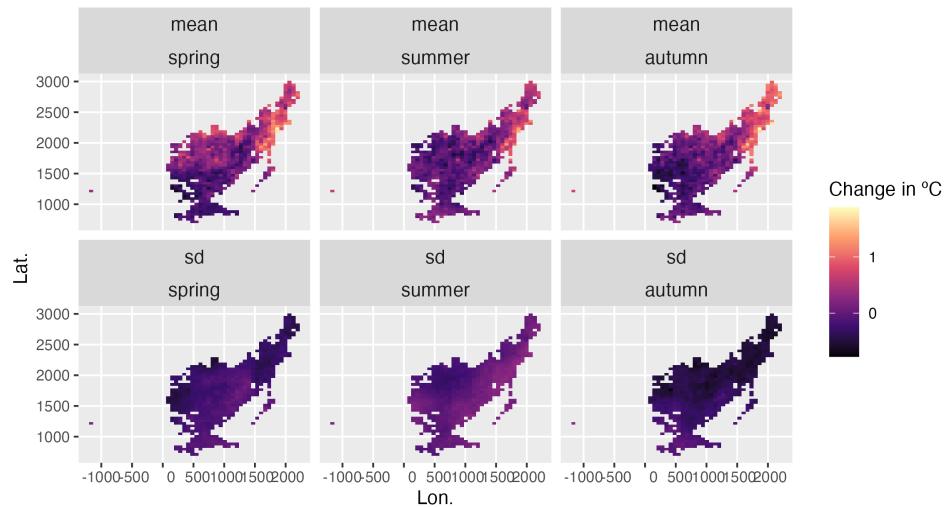


Figure A12: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *A. hyemalis* used in post-hoc climate correlation analysis.

A



B

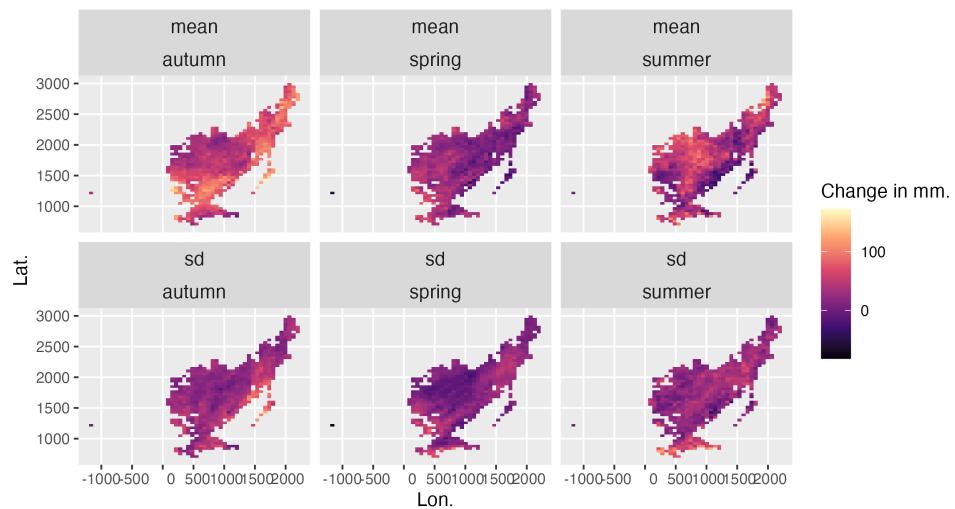
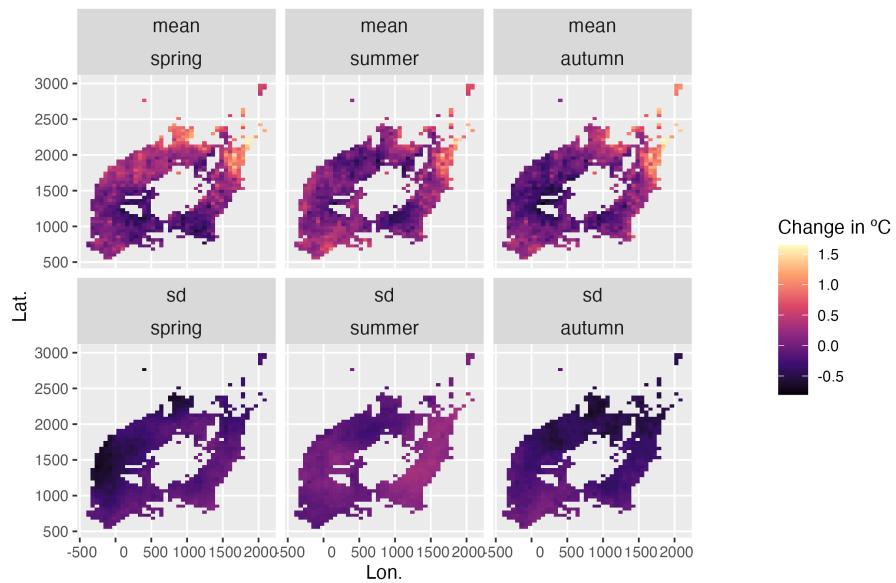


Figure A13: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020.

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

A



B

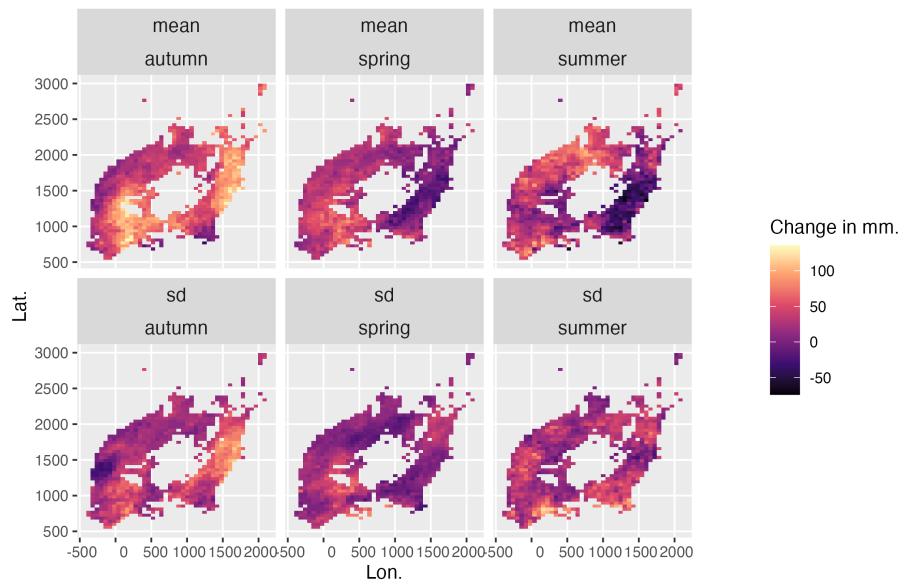


Figure A14: Change in seasonal climate variables between the periods 1895-1925 and 1990-2020. Color represents change in (A) seasonal temperature and (B) seasonal precipitation. Maps show pixels covering the modeled distribution of *E. virginicus* used in post-hoc climate correlation analysis.

Table A1: Summary of herbarium samples across collections

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

509

Literature Cited

- 510 Michelle E Afkhami. Fungal endophyte–grass symbioses are rare in the California floristic
 511 province and other regions with mediterranean-influenced climates. *Fungal ecology*, 5(3):345–
 512 352, 2012.
- 513 Michelle E Afkhami and Jennifer A Rudgers. Symbiosis lost: imperfect vertical transmission of
 514 fungal endophytes in grasses. *The American Naturalist*, 172(3):405–416, 2008.
- 515 Michelle E Afkhami, Patrick J McIntyre, and Sharon Y Strauss. Mutualist-mediated effects on
 516 species' range limits across large geographic scales. *Ecology letters*, 17(10):1265–1273, 2014.
- 517 Sally N Aitken, Sam Yeaman, Jason A Holliday, Tongli Wang, and Sierra Curtis-McLane. Adap-
 518 tation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary
 519 applications*, 1(1):95–111, 2008.

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

- 544 Michael Bradshaw, Uwe Braun, Marianne Elliott, Julia Kruse, Shu-Yan Liu, Guanxiu Guan, and
545 Patrick Tobin. A global genetic analysis of herbarium specimens reveals the invasion dynamics
546 of an introduced plant pathogen. *Fungal Biology*, 125(8):585–595, 2021.
- 547 D Brem and A Leuchtmann. Epichloë grass endophytes increase herbivore resistance in the
548 woodland grass *brachypodium sylvaticum*. *Oecologia*, 126(4):522–530, 2001.
- 549 Tamara A Carleton and Solomon M Hsiang. Social and economic impacts of climate. *Science*, 353
550 (6304):aad9837, 2016.
- 551 Shen Cheng, Ying-Ning Zou, Kamil Kuča, Abeer Hashem, Elsayed Fathi Abd_Allah, and Qiang-
552 Sheng Wu. Elucidating the mechanisms underlying enhanced drought tolerance in plants
553 mediated by arbuscular mycorrhizal fungi. *Frontiers in Microbiology*, 12:4029, 2021.
- 554 Keith Clay and Christopher Schardl. Evolutionary origins and ecological consequences of endo-
555 phyte symbiosis with grasses. *the american naturalist*, 160(S4):S99–S127, 2002.
- 556 David G Clayton, Luisa Bernardinelli, and Cristina Montomoli. Spatial correlation in ecological
557 analysis. *International journal of epidemiology*, 22(6):1193–1202, 1993.
- 558 KD Craven, PTW Hsiao, A Leuchtmann, W Hollin, and CL Schardl. Multigene phylogeny of
559 epichloë species, fungal symbionts of grasses. *Annals of the Missouri Botanical Garden*, pages
560 14–34, 2001.
- 561 Kerri M Crawford, John M Land, and Jennifer A Rudgers. Fungal endophytes of native grasses
562 decrease insect herbivore preference and performance. *Oecologia*, 164:431–444, 2010.
- 563 Michael S Crossley, Timothy D Meehan, Matthew D Moran, Jeffrey Glassberg, William E Snyder,
564 and Andrew K Davis. Opposing global change drivers counterbalance trends in breeding north
565 american monarch butterflies. *Global change biology*, 28(15):4726–4735, 2022.
- 566 Christopher Daly and Kirk Bryant. The prism climate and weather system—an introduction.
567 *Corvallis, OR: PRISM climate group*, 2, 2013.

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

- 593 AE Douglas. Host benefit and the evolution of specialization in symbiosis. *Heredity*, 81(6):599–
594 603, 1998.
- 595 Yuan-Wen Duan, Haibao Ren, Tao Li, Lin-Lin Wang, Zhi-Qiang Zhang, Yan-Li Tu, and Yong-Ping
596 Yang. A century of pollination success revealed by herbarium specimens of seed pods. *New*
597 *Phytologist*, 224(4):1512–1517, 2019.
- 598 Erika J Edwards, Brent D Mishler, and Charles D Davis. University herbaria are uniquely impor-
599 tant. *Trends in Plant Science*.
- 600 Markus Engel, Tobias Mette, and Wolfgang Falk. Spatial species distribution models: Using
601 bayes inference with inla and spde to improve the tree species choice for important european
602 tree species. *Forest Ecology and Management*, 507:119983, 2022.
- 603 Sanne M Evers, Tiffany M Knight, David W Inouye, Tom EX Miller, Roberto Salguero-Gómez,
604 Amy M Iler, and Aldo Compagnoni. Lagged and dormant season climate better predict plant
605 vital rates than climate during the growing season. *Global Change Biology*, 27(9):1927–1941,
606 2021.
- 607 Paul EM Fine. Vectors and vertical transmission: an epidemiologic perspective. *Annals of the New*
608 *York Academy of Sciences*, 266(1):173–194, 1975.
- 609 Joshua C Fowler, Shaun Ziegler, Kenneth D Whitney, Jennifer A Rudgers, and Tom EX Miller.
610 Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity.
611 *Ecology Letters*, 27(5):e14438, 2024.
- 612 PR Frade, F De Jongh, F Vermeulen, J Van Bleijswijk, and RPM Bak. Variation in symbiont
613 distribution between closely related coral species over large depth ranges. *Molecular Ecology*,
614 17(2):691–703, 2008.
- 615 Sarah E Gilman, Mark C Urban, Joshua Tewksbury, George W Gilchrist, and Robert D Holt. A

- 616 framework for community interactions under climate change. *Trends in ecology & evolution*, 25
617 (6):325–331, 2010.
- 618 Gustaf Granath, Mark Vicari, Dawn R Bazely, John P Ball, Adriana Puentes, and Tomo Rakoce-
619 vic. Variation in the abundance of fungal endophytes in fescue grasses along altitudinal and
620 grazing gradients. *Ecography*, 30(3):422–430, 2007.
- 621 Andrin Gross, Célia Petitcollin, Cyril Dutech, Bayo Ly, Marie Massot, Julie Faivre d’Arcier, Laure
622 Dubois, Gilles Saint-Jean, and Marie-Laure Desprez-Loustau. Hidden invasion and niche con-
623 traction revealed by herbaria specimens in the fungal complex causing oak powdery mildew
624 in europe. *Biological Invasions*, 23:885–901, 2021.
- 625 Edmund M. Hart and Kendon Bell. prism: Download data from the oregon prism project. 2015.
626 doi: 10.5281/zenodo.33663. URL <https://github.com/ropensci/prism>. R package version
627 0.0.6.
- 628 J Mason Heberling and David J Burke. Utilizing herbarium specimens to quantify historical
629 mycorrhizal communities. *Applications in plant sciences*, 7(4):e01223, 2019.
- 630 Robert J Hijmans and Catherine H Graham. The ability of climate envelope models to predict the
631 effect of climate change on species distributions. *Global change biology*, 12(12):2272–2281, 2006.
- 632 Robert J Hijmans, Steven Phillips, John Leathwick, Jane Elith, and Maintainer Robert J Hijmans.
633 Package ‘dismo’. *Circles*, 9(1):1–68, 2017.
- 634 Janneke HilleRisLambers, Melanie A Harsch, Ailene K Ettinger, Kevin R Ford, and Elinore J
635 Theobald. How will biotic interactions influence climate change-induced range shifts? *Annals*
636 *of the New York Academy of Sciences*, 1297(1):112–125, 2013.
- 637 IPCC. Climate change 2021: The physical science basis, 2021. URL
638 <https://www.ipcc.ch/report/ar6/wg1/>.

- 639 Nick JB Isaac, Marta A Jarzyna, Petr Keil, Lea I Dambly, Philipp H Boersch-Supan, Ella Browning,
640 Stephen N Freeman, Nick Golding, Gurutzeta Guillera-Arroita, Peter A Henrys, et al. Data
641 integration for large-scale models of species distributions. *Trends in ecology & evolution*, 35(1):
642 56–67, 2020.
- 643 Alberto Jiménez-Valverde. Insights into the area under the receiver operating characteristic curve
644 (auc) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeog-*
645 *raphy*, 21(4):498–507, 2012.
- 646 David Kahle, Hadley Wickham, and Maintainer David Kahle. Package ‘ggmap’. *Retrieved Septem-*
647 *ber*, 5:2021, 2019.
- 648 Melanie R Kazenel, Catherine L Debban, Luciana Ranelli, Will Q Hendricks, Y Anny Chung,
649 Thomas H Pendergast IV, Nikki D Charlton, Carolyn A Young, and Jennifer A Rudgers. A
650 mutualistic endophyte alters the niche dimensions of its host plant. *AoB plants*, 7:plv005, 2015.
- 651 Roland A Knapp, Gary M Fellers, Patrick M Kleeman, David AW Miller, Vance T Vredenburg,
652 Erica Bree Rosenblum, and Cheryl J Briggs. Large-scale recovery of an endangered amphibian
653 despite ongoing exposure to multiple stressors. *Proceedings of the National Academy of Sciences*,
654 113(42):11889–11894, 2016.
- 655 Mikhail V Kozlov, Irina V Sokolova, Vitali Zverev, Alexander A Egorov, Mikhail Y Goncharov,
656 and Elena L Zvereva. Biases in estimation of insect herbivory from herbarium specimens.
657 *Scientific Reports*, 10(1):12298, 2020.
- 658 Benjamin R Lee, Evelyn F Alecrim, Tara K Miller, Jessica RK Forrest, J Mason Heberling,
659 Richard B Primack, and Risa D Sargent. Phenological mismatch between trees and wildflow-
660 ers: Reconciling divergent findings in two recent analyses. *Journal of Ecology*, 112(6):1184–1199,
661 2024.
- 662 James Lendemer, Barbara Thiers, Anna K Monfils, Jennifer Zaspel, Elizabeth R Ellwood, Andrew
663 Bentley, Katherine LeVan, John Bates, David Jennings, Dori Contreras, et al. The extended

- 664 specimen network: A strategy to enhance us biodiversity collections, promote research and
665 education. *BioScience*, 70(1):23–30, 2020.
- 666 A Leuchtmann. Systematics, distribution, and host specificity of grass endophytes. *Natural toxins*,
667 1(3):150–162, 1992.
- 668 Adrian Leuchtmann, Charles W Bacon, Christopher L Schardl, James F White Jr, and Mariusz
669 Tadych. Nomenclatural realignment of neotyphodium species with genus epichloë. *Mycologia*,
670 106(2):202–215, 2014.
- 671 Finn Lindgren, Håvard Rue, and Johan Lindström. An explicit link between gaussian fields and
672 gaussian markov random fields: the stochastic partial differential equation approach. *Journal
673 of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4):423–498, 2011.
- 674 Canran Liu, Pam M Berry, Terence P Dawson, and Richard G Pearson. Selecting thresholds of
675 occurrence in the prediction of species distributions. *Ecography*, 28(3):385–393, 2005.
- 676 Margaret McFall-Ngai, Michael G Hadfield, Thomas CG Bosch, Hannah V Carey, Tomislav
677 Domazet-Lošo, Angela E Douglas, Nicole Dubilier, Gerard Eberl, Tadashi Fukami, Scott F
678 Gilbert, et al. Animals in a bacterial world, a new imperative for the life sciences. *Proceedings
679 of the National Academy of Sciences*, 110(9):3229–3236, 2013.
- 680 Timothy D Meehan, Nicole L Michel, and Håvard Rue. Spatial modeling of audubon christmas
681 bird counts reveals fine-scale patterns and drivers of relative abundance trends. *Ecosphere*, 10
682 (4):e02707, 2019.
- 683 Emily K Meineke, Charles C Davis, and T Jonathan Davies. The unrealized potential of herbaria
684 for global change biology. *Ecological Monographs*, 88(4):505–525, 2018.
- 685 Emily K Meineke, Aimée T Classen, Nathan J Sanders, and T Jonathan Davies. Herbarium
686 specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1):105–117,
687 2019.

- 688 Abigail R Meyer, Maria Valentin, Laima Liulevicius, Tami R McDonald, Matthew P Nelsen, Jean
689 Pengra, Robert J Smith, and Daniel Stanton. Climate warming causes photobiont degradation
690 and c starvation in a boreal climate sentinel lichen. *American Journal of Botany*, 2022.
- 691 David AW Miller, Krishna Pacifici, Jamie S Sanderlin, and Brian J Reich. The recent past and
692 promising future for data integration methods to estimate species' distributions. *Methods in*
693 *Ecology and Evolution*, 10(1):22–37, 2019.
- 694 Daniel S Park, Ian Breckheimer, Alex C Williams, Edith Law, Aaron M Ellison, and Charles C
695 Davis. Herbarium specimens reveal substantial and unexpected variation in phenological sen-
696 sitivity across the eastern united states. *Philosophical Transactions of the Royal Society B*, 374
697 (1763):20170394, 2019.
- 698 Martin Parniske. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Reviews*
699 *Microbiology*, 6(10):763–775, 2008.
- 700 Anton Pauw and Julie A Hawkins. Reconstruction of historical pollination rates reveals linked
701 declines of pollinators and plants. *Oikos*, 120(3):344–349, 2011.
- 702 Shilong Piao, Qiang Liu, Anping Chen, Ivan A Janssens, Yongshuo Fu, Junhu Dai, Lingli Liu,
703 XU Lian, Miaogen Shen, and Xiaolin Zhu. Plant phenology and global climate change: Current
704 progresses and challenges. *Global change biology*, 25(6):1922–1940, 2019.
- 705 Timothée Poisot, Gabriel Bergeron, Kevin Cazelles, Tad Dallas, Dominique Gravel, Andrew Mac-
706 Donald, Benjamin Mercier, Clément Violet, and Steve Vissault. Global knowledge gaps in
707 species interaction networks data. *Journal of Biogeography*, 48(7):1552–1563, 2021.
- 708 Nicole E Rafferty, Paul J CaraDonna, and Judith L Bronstein. Phenological shifts and the fate of
709 mutualisms. *Oikos*, 124(1):14–21, 2015.
- 710 Christopher J Raxworthy and Brian Tilston Smith. Mining museums for historical dna: advances
711 and challenges in museomics. *Trends in Ecology & Evolution*, 36(11):1049–1060, 2021.

- 712 François Renoz, Inès Pons, and Thierry Hance. Evolutionary responses of mutualistic insect–
713 bacterial symbioses in a world of fluctuating temperatures. *Current opinion in insect science*, 35:
714 20–26, 2019.
- 715 Elizabeth Lewis Roberts and Aileen Ferraro. Rhizosphere microbiome selection by epichloë en-
716 dophytes of *festuca arundinacea*. *Plant and soil*, 396:229–239, 2015.
- 717 RJ Rodriguez, JF White Jr, Anne E Arnold, and a RS and Redman. Fungal endophytes: diversity
718 and functional roles. *New phytologist*, 182(2):314–330, 2009.
- 719 Gregor Rolshausen, Francesco Dal Grande, Anna D Sadowska-Deś, Jürgen Otte, and Imke
720 Schmitt. Quantifying the climatic niche of symbiont partners in a lichen symbiosis indicates
721 mutualist-mediated niche expansions. *Ecography*, 41(8):1380–1392, 2018.
- 722 Jennifer A Rudgers and Angela L Swafford. Benefits of a fungal endophyte in *elymus virginicus*
723 decline under drought stress. *Basic and Applied Ecology*, 10(1):43–51, 2009.
- 724 Jennifer A Rudgers, Michelle E Afkhami, Megan A Rúa, Andrew J Davitt, Samantha Hammer,
725 and Valérie M Huguet. A fungus among us: broad patterns of endophyte distribution in the
726 grasses. *Ecology*, 90(6):1531–1539, 2009.
- 727 Jennifer A Rudgers, Rebecca A Fletcher, Eric Olivas, Carolyn A Young, Nikki D Charlton, Dean E
728 Pearson, and John L Maron. Long-term ungulate exclusion reduces fungal symbiont prevalence
729 in native grasslands. *Oecologia*, 181:1151–1161, 2016.
- 730 Håvard Rue, Sara Martino, and Nicolas Chopin. Approximate bayesian inference for latent gaus-
731 sian models by using integrated nested laplace approximations. *Journal of the royal statistical
732 society: Series b (statistical methodology)*, 71(2):319–392, 2009.
- 733 Kari Saikkonen, Pedro E Gundel, and Marjo Helander. Chemical ecology mediated by fungal
734 endophytes in grasses. *Journal of chemical ecology*, 39:962–968, 2013.

- 735 Michelle E Sneck, Jennifer A Rudgers, Carolyn A Young, and Tom EX Miller. Variation in the
736 prevalence and transmission of heritable symbionts across host populations in heterogeneous
737 environments. *Microbial Ecology*, 74:640–653, 2017.
- 738 Thomas F Stocker, Dahe Qin, G-K Plattner, Lisa V Alexander, Simon K Allen, Nathaniel L Bindoff,
739 F-M Bréon, John A Church, Ulrich Cubasch, Seita Emori, et al. Technical summary. In *Climate
740 change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment
741 Report of the Intergovernmental Panel on Climate Change*, pages 33–115. Cambridge University
742 Press, 2013.
- 743 Peter A Stott, Nathan P Gillett, Gabriele C Hegerl, David J Karoly, Dáithí A Stone, Xuebin Zhang,
744 and Francis Zwiers. Detection and attribution of climate change: a regional perspective. *Wiley
745 interdisciplinary reviews: climate change*, 1(2):192–211, 2010.
- 746 S Sully, DE Burkepile, MK Donovan, G Hodgson, and R Van Woesik. A global analysis of coral
747 bleaching over the past two decades. *Nature communications*, 10(1):1–5, 2019.
- 748 E Toby Kiers, Todd M Palmer, Anthony R Ives, John F Bruno, and Judith L Bronstein. Mutualisms
749 in a changing world: an evolutionary perspective. *Ecology letters*, 13(12):1459–1474, 2010.
- 750 Andrew T Tredennick, Giles Hooker, Stephen P Ellner, and Peter B Adler. A practical guide to
751 selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102(6):e03336,
752 2021.
- 753 Amy M Truitt, Martin Kapun, Rupinder Kaur, and Wolfgang J Miller. Wolbachia modifies thermal
754 preference in drosophila melanogaster. *Environmental microbiology*, 21(9):3259–3268, 2019.
- 755 Shripad D. Tuljapurkar. Population dynamics in variable environments. III. Evo-
756 lutionary dynamics of r-selection. *Theoretical Population Biology*, 21(1):141–165,
757 February 1982. ISSN 0040-5809. doi: 10.1016/0040-5809(82)90010-7. URL
758 <http://www.sciencedirect.com/science/article/pii/0040580982900107>.

- 759 Arantxa Urdangarin, Tomás Goicoa, and María Dolores Ugarte. Evaluating recent methods to
760 overcome spatial confounding. *Revista Matemática Complutense*, 36(2):333–360, 2023.
- 761 Veronika Vikuk, Carolyn A Young, Stephen T Lee, Padmaja Nagabhyru, Markus Krischke, Mar-
762 tin J Mueller, and Jochen Krauss. Infection rates and alkaloid patterns of different grass species
763 with systemic epichloë endophytes. *Applied and Environmental Microbiology*, 85(17):e00465–19,
764 2019.
- 765 Zhengfeng Wang, Chunjie Li, and James White. Effects of epichloë endophyte infection on
766 growth, physiological properties and seed germination of wild barley under saline conditions.
767 *Journal of Agronomy and Crop Science*, 206(1):43–51, 2020.
- 768 Robert J Warren and Mark A Bradford. Mutualism fails when climate response differs between
769 interacting species. *Global Change Biology*, 20(2):466–474, 2014.
- 770 Nicole S Webster, Rose E Cobb, and Andrew P Negri. Temperature thresholds for bacterial
771 symbiosis with a sponge. *The ISME journal*, 2(8):830–842, 2008.
- 772 James F White and Garry T Cole. Endophyte-host associations in forage grasses. i. distribution
773 of fungal endophytes in some species of lolium and festuca. *Mycologia*, 77(2):323–327, 1985.
- 774 Franziska M Willems, JF Scheepens, and Oliver Bossdorf. Forest wildflowers bloom earlier as
775 europe warms: lessons from herbaria and spatial modelling. *New Phytologist*, 235(1):52–65,
776 2022.
- 777 Charles G Willis, Elizabeth R Ellwood, Richard B Primack, Charles C Davis, Katelin D Pearson,
778 Amanda S Gallinat, Jenn M Yost, Gil Nelson, Susan J Mazer, Natalie L Rossington, et al. Old
779 plants, new tricks: Phenological research using herbarium specimens. *Trends in ecology &*
780 *evolution*, 32(7):531–546, 2017.
- 781 Chao Xia, Nana Li, Yawen Zhang, Chunjie Li, Xingxu Zhang, and Zhibiao Nan. Role of epichloë

⁷⁸² endophytes in defense responses of cool-season grasses to pathogens: A review. *Plant disease*,
⁷⁸³ 102(11):2061–2073, 2018.

⁷⁸⁴ Kentaro Yoshida, Eriko Sasaki, and Sophien Kamoun. Computational analyses of ancient
⁷⁸⁵ pathogen dna from herbarium samples: challenges and prospects. *Frontiers in plant science*,
⁷⁸⁶ 6:771, 2015.