

<sup>1</sup> Increasing prevalence of plant-fungal symbiosis across two  
<sup>2</sup> centuries of environmental change

<sup>3</sup> Joshua C. Fowler<sup>1,2\*</sup>

Jacob Moutouama<sup>1</sup>

Tom E. X. Miller<sup>1</sup>

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

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

<sup>9</sup> *Keywords:* .

<sup>10</sup> *Manuscript type:* Article.

<sup>11</sup> Prepared using the suggested L<sup>A</sup>T<sub>E</sub>X template for *Am. Nat.*

---

<sup>1</sup> *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 drivers<sup>2</sup> 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.<sup>3</sup>

---

<sup>2</sup>Describe "changes" – warming? drying?

<sup>3</sup>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

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.<sup>4</sup> 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

---

<sup>4</sup>Edited 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.<sup>5</sup>

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 heterogenous are temporal trends in endophyte  
118 prevalence across eastern North America? We then address how climate change may be driv-  
119 ing trends in endophyte prevalence by asking: (iii) What is the relationship between variation  
120 in temporal trends in endophyte prevalence and changes in climate drivers? We predicted that  
121 aggregate endophyte prevalence would increase over time in tandem with climate warming, and  
122 that hotspots of endophyte change would correspond spatially to hotspots of climate change.  
123 Finally, we evaluated the performance of models built on data from historic specimens with an  
124 out-of-sample test, data on endophyte prevalence from contemporary surveys of host popula-  
125 tions. To answer these questions we examined a total of 2,346 specimens collected across eastern  
126 North America between 1824 and 2019.<sup>6</sup>

## 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 C<sub>3</sub> 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.

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

<sup>144</sup> *Herbarium surveys*

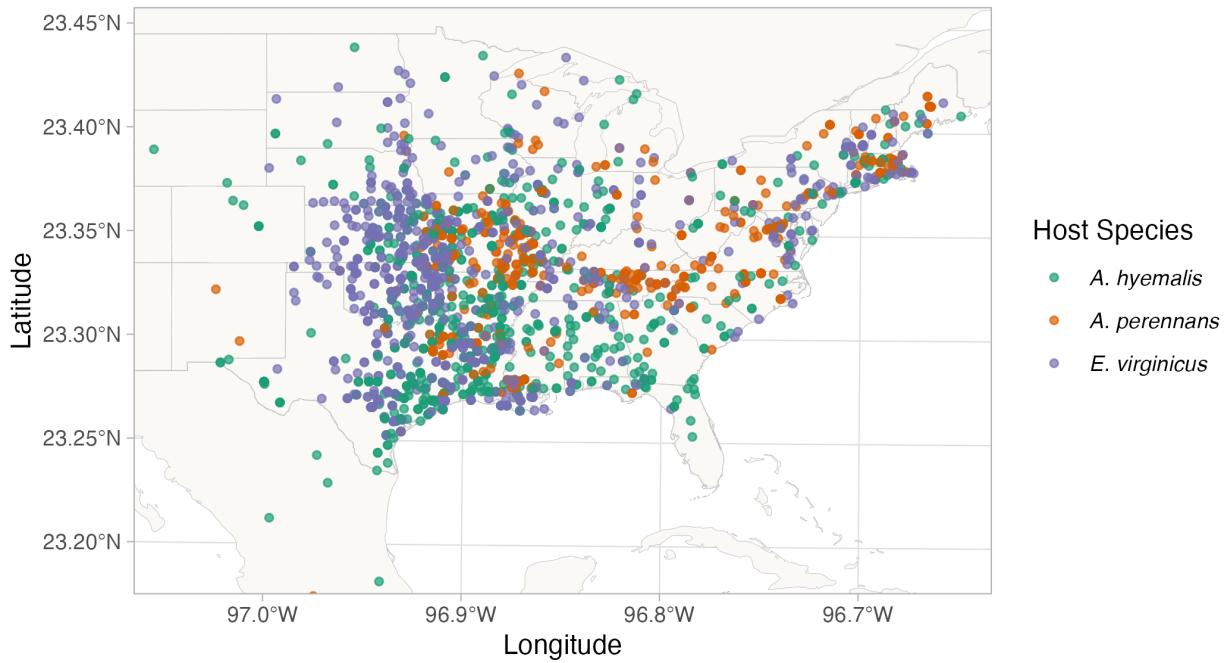
<sup>145</sup> We visited nine herbaria between 2019 and 2022 (see Table A1 for a summary of specimens in-  
<sup>146</sup> cluded from each collection). With permission from herbarium staff, we acquired seed samples  
<sup>147</sup> from 1135 *A. hyemalis* specimens collected between 1824 and 2019,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

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

<sup>162</sup> After collecting seed samples, we quantified the presence or absence of *Epichloë* fungal hy-  
<sup>163</sup> phae, which grow intercellularly, in each specimen using microscopy. We first softened seeds  
<sup>164</sup> with a 10% NaOH solution, then stained the seeds with aniline blue-lactic acid stain and squashed  
<sup>165</sup> them under a microscope cover slip. We examined the squashed seeds for the presence of fungal  
<sup>166</sup> hyphae at 200-400X magnification (Bacon and White, 2018). In some cases, the tissues examined  
<sup>167</sup> during microscopy came from flowers or otherwise non-viable seeds, which were excluded for  
<sup>168</sup> that specimen. On average we scored 4.7 seeds per specimen of *A. hyemalis*, 4.2 seeds per spec-  
<sup>169</sup> imen of *A. perennans*, and 3.8 seeds per specimen of *E. virginicus*; we scored # seeds in total. .  
<sup>170</sup> Due to imperfect vertical transmission (Afkhami and Rudgers, 2008), it is possible that symbiotic  
<sup>171</sup> host-plants produce a mixture of symbiotic and non-symbiotic seeds. We therefore designated a  
<sup>172</sup> specimen as endophyte-symbiotic if *Epichloë* hyphae were observed in one or more of its seeds,  
<sup>173</sup> or non-symbiotic if hyphae were observed in none of its seeds. To capture uncertainty in the  
<sup>174</sup> endophyte scoring process, we recorded both a "liberal" and a "conservative" endophyte status  
<sup>175</sup> for each plant specimen. When we identified potential endophytes with unusual morphology,  
<sup>176</sup> low uptake of stain, or a small amount of fungal hyphae across the scored seeds, we recorded a  
<sup>177</sup> positive liberal status (more likely to be endophyte-positive) and a negative conservative status  
<sup>178</sup> (less likely to be endophyte-positive). 89% of scored plants had matching liberal and conservative  
<sup>179</sup> scores, reflecting high confidence in endophyte status. The following analyses in the main text  
<sup>180</sup> used the liberal status, but we repeated all analyses with the conservative status which yielded  
<sup>181</sup> qualitatively similar results (Fig. A11)

<sup>182</sup> *Modeling spatial and temporal changes in endophyte prevalence*

<sup>183</sup> We assessed spatial and temporal changes in endophyte prevalence across each host distribution,  
<sup>184</sup> quantifying the "global" temporal trends, aggregating across space, and then examining spatial  
<sup>185</sup> 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 occurrences<sup>7</sup>, 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

---

<sup>7</sup> spelling?

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

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

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

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

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

$$(1d)$$

<sup>214</sup> Previous work suggests that behavior of historical botanists and uneven sampling may intro-  
<sup>215</sup> duce biases into ecological inferences made from historic collections (Kozlov et al., 2020). Prolific  
<sup>216</sup> collectors who contribute thousands of specimens may be more or less likely to collect certain  
<sup>217</sup> 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,  $\chi$  and  $\omega$ , 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 XX<sup>8</sup> 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).**<sup>9</sup> <sup>10</sup> 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

<sup>9</sup> *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.*

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

<sup>241</sup> (2017), and surveys of *A. hyemalis* took place between 2015 and 2020<sup>11</sup>. Population surveys of *A.*  
<sup>242</sup> *hyemalis* were initially designed to cover longitudinal variation in endophyte prevalence towards  
<sup>243</sup> its range edge, while surveys of *E. virginicus* were designed to cover latitudinal variation along its  
<sup>244</sup> range edge. In total, we visited 43 populations of *A. hyemalis* and 20 populations of *E. virginicus*  
<sup>245</sup> across the south-central US, with emphasis on Texas and neighboring states (Fig A7). During  
<sup>246</sup> surveys, we collected seeds from up to 30 individuals per location (average number of plants  
<sup>247</sup> sampled: 22.9). We quantified the endophyte status of each individual with staining microscopy  
<sup>248</sup> as described for the herbarium surveys (with 5-10 seeds scored per individual), and calculated  
<sup>249</sup> the prevalence of endophytes within the population (proportion of symbiotic plants divided by  
<sup>250</sup> the number of sampled plants). For each population, we compared the observed fraction of  
<sup>251</sup> endophyte-symbiotic hosts to the predicted probability of endophyte occurrence  $\hat{P}$  derived from  
<sup>252</sup> the model based on location and year. The contemporary survey period (2013-2020) is at the most  
<sup>253</sup> recent edge of the time period encompassed by the historical observations used for model fitting.  
<sup>254</sup> We compared the model's prediction for these locations to the observed population prevalence.

<sup>255</sup> *Assessing the role of climate drivers*

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

---

<sup>11</sup> *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.*

sons within the year (Spring: January, February, March, April; Summer: May, June, July, August; Autumn: September, October, November, December). This division of seasons allowed us to quantify differences in climate associated with the two “cool” seasons, when we expect our focal species to be most biologically active (*A. hyemalis* flowering phenology: Spring; *E. virginicus*: Spring and Summer; *A. perennans*: Fall). In addition to mean climate conditions, environmental variability itself can influence population dynamics (Tuljapurkar, 1982) and changes in variability are a key prediction of climate change models (IPCC, 2021; Stocker et al., 2013). Therefore we calculated the coefficient of variation (CV) during each period for each annual and seasonal climate driver as the interannual standard deviation divided by the mean across each 30-year period. We then took the difference between recent and historic periods for the mean and CV for each climate driver (Fig. A5)<sup>12</sup>. Because initial analyses indicated a high degree of collinearity between seasonal and annual changes in temperature, we used annual temperature only, along with annual and seasonal precipitation, in the subsequent analysis. All together, this left us with measurements of change in 10 potential climate drivers: the mean and coefficient of variation of annual temperature, as well as the mean and coefficient of variation of cumulative annual precipitation, cumulative spring precipitation, cumulative summer precipitation, and cumulative autumn precipitation (Fig A8-A9)<sup>13</sup>.

To evaluate whether areas that have experienced the greatest changes in endophyte prevalence (hotspots of endophyte change) are associated with high degrees of change in climate (hotspots of climate change), we modeled spatially varying slopes of endophyte change through time ( $\beta_1$ ) as a linear function of environmental covariates, with a Gaussian error distribution.<sup>14</sup> Calculating correlations from many pixels across the study region risks artificially inflating confidence in our results due to large sample sizes, and so we repeated this calculation using only a

<sup>12</sup>This is Figure A7 – Can you make the color scale on these diverging at zero?

<sup>13</sup>The species names are not clear on Fig A9. I suggest increase the font siize

<sup>14</sup>I 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 disrtibution.

288 random subsample of 100 pixels across the study region<sup>15</sup>. <sup>16</sup> <sup>17</sup>

289 *Modeling distributions of host species*

290 We modeled the distribution of each host species to generate maps on which we predicted the  
291 dynamics of *Epichloë* symbionts. We followed the ODMAP (overview, data, model, assessment,  
292 prediction) protocol (Crossley et al., 2022), using presence-only observations of the host species  
293 from GBIF between 1990 to 2020<sup>18</sup>. To reduce the potential influence of sampling bias and spa-  
294 tial autocorrelation, we thinned the occurrences to the spatial scale ()<sup>19</sup> of our selected climatic  
295 predictors. We selected climate variables that aligned with our analysis of climatic influences on  
296 trends in endophyte prevalence described above. We calculated the mean and standard deviation  
297 of seasonal temperature and precipitation across 1990 to 2020. Among this suite of variables,  
298 we chose to include mean spring temperature, mean spring precipitation, and mean summer  
299 temperature<sup>20</sup>, which were uncorrelated (Variance Inflation Factor > 0.7) and allowed us to pre-  
300 dict the occurrence probability of each host species in space and time. We fit maximum entropy  
301 (MaxEnt) models using the maxent function in the package dismo (Hijmans et al., 2017). Max-  
302 Ent is preferred because it has been shown to generate response curves with less unpredictable  
303 behavior when applied to new climates (Hijmans and Graham, 2006).<sup>21</sup> We generated 10,000  
304 pseudo-absences as background points, and split the occurrence data into 75% for model train-

---

<sup>15</sup> 100 seems like a low number to me. What if we did this for all of the herbarium collection locations?

<sup>16</sup> Are the methods above repeated for each species separately?

<sup>17</sup> I 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.

<sup>18</sup> How many data points does this end up being?

<sup>19</sup> I think this is 4km, but need to check

<sup>20</sup> is 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

<sup>21</sup> possibly could remove this sentence?

305 ing and 25% for model testing. The performance of models was evaluated with AUC AUC<sup>22</sup>  
306 (Jiménez-Valverde, 2012). To convert the continuous predicted probabilities into binary presence  
307 - absence maps, we used the training sensitivity (true positive rate) and specificity threshold  
308 (true negative rate) (Liu et al., 2005). These binary maps serve as boundaries in presented maps  
309 of change in endophyte prevalence, and outline the set of pixels used in our analysis of climate  
310 correlates with trends in endophyte prevalence

311 **Results**

312 *How has endophyte prevalence changed over time?*

313 We found that endophyte prevalence increased within the examined specimens over the last  
314 two centuries for all three host species (Fig. 4). On average, *A. hyemalis* and *E. virginicus* both  
315 increased from 30 % to over 70% prevalence across the study region, and *A. perennans* increased  
316 from 15% to over 70% prevalence. Our model indicates a higher certainty that overall temporal  
317 trends are positive for *A. hyemalis* and *A. perennans* than for *E. virginicus* (99% probability of a  
318 positive overall year slope in *A. hyemalis*, 89% probability of a positive overall year slope in *A.*  
319 *perennans*, and 58% probability of a positive overall year slope in *E. virginicus*).<sup>23</sup>

---

<sup>22</sup>can we add these values?

<sup>23</sup>These numbers are currently outdated. I am making some adjustments to models, and will update with final model

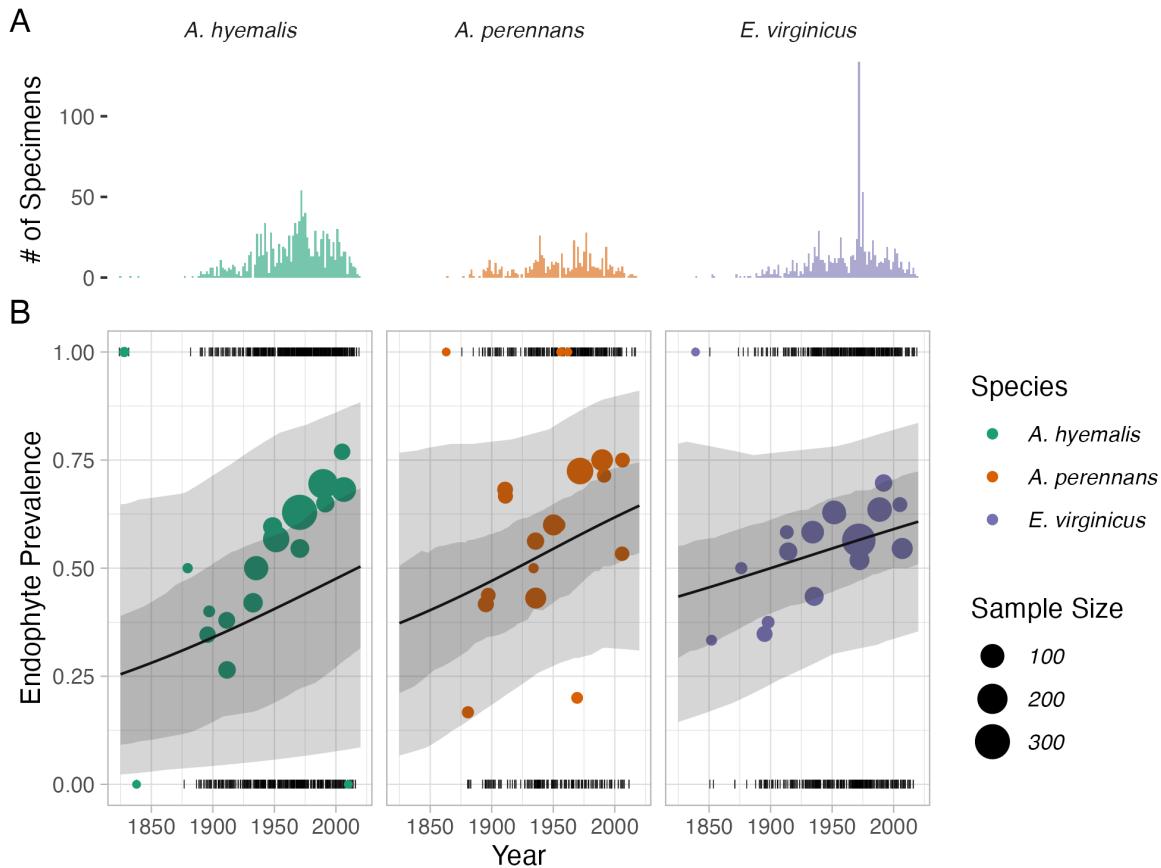


Figure 2: Temporal trends in endophyte prevalence. (A) Histograms show the frequency of collection through time for each host species. (B) Colored points are binned means of the observed endophyte presence/absence data (black dashes). Colors represent each host species and point size is determined by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

320      *How spatially heterogeneous are temporal trends in endophyte prevalence?*

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

*hyemalis* and *A. perennans* experienced increases in percent prevalence by as much as 4% per year over the study period, while *E. virginicus* experienced increases up to around 1.5 % per year. In other regions, there were negligible changes. Notably, the symbionts of *E. virginicus* experienced only slight increases in prevalence, and were less spatially variable than the other two species. Regions that start with low endophyte prevalence, as in the southwestern portion of the range of *A. hyemalis*(Fig. A1), also experienced negligible change, suggesting that this may be driven more by the absence of the endophyte.<sup>24</sup> Predicted trends for *A. perennans* show certain areas of both large increase and of large decrease, however this species, for which we have the fewest samples, has the largest uncertainty. The posterior estimates of our spatially varying temporal trends, indicate relatively narrow certainty (need to compute<sup>25</sup>).

---

<sup>24</sup>more discussion material, but putting it here for now.

<sup>25</sup>

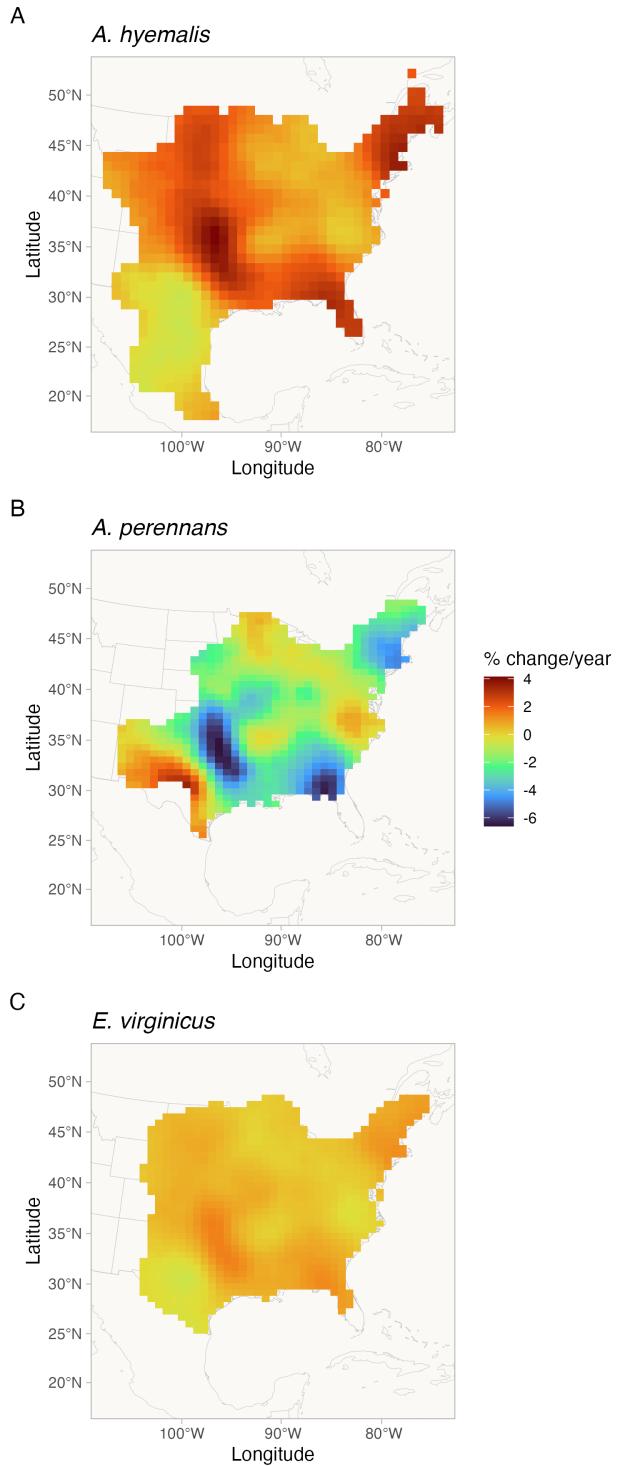
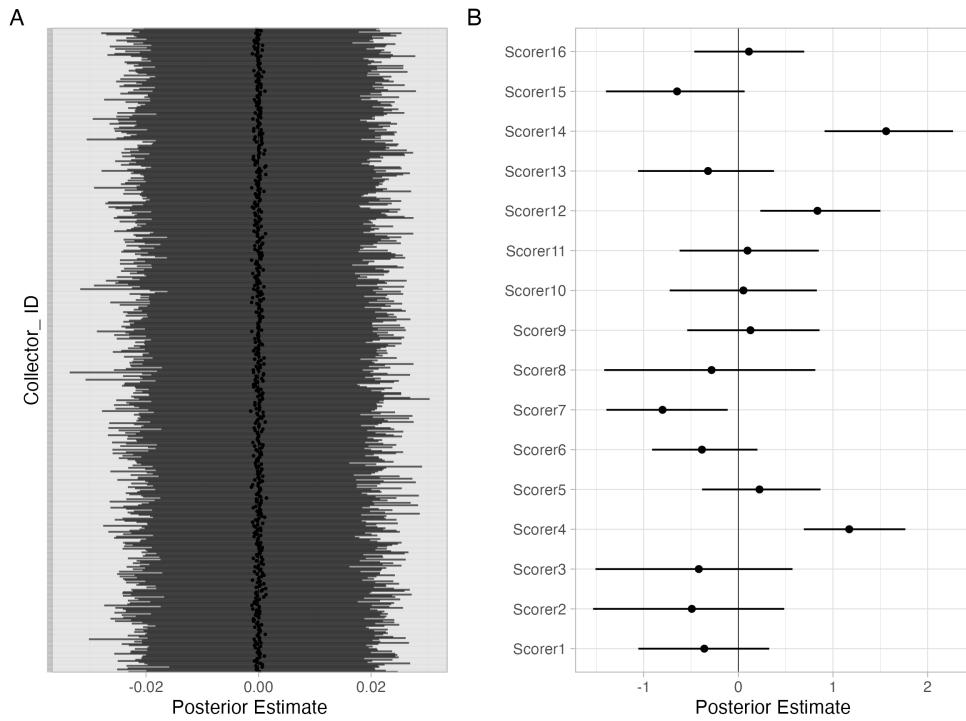


Figure 3: Predicted posterior mean of spatially-varying slopes representing change in endophyte prevalence for each host species. Color indicates the relative change in predicted endophyte prevalence.

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

335    We quantified temporal and spatial trends in endophyte prevalence while accounting for poten-  
336    tial biases introduced by collectors and by individuals who quantified endophyte presence/absence  
337    with the use of random effects. We found no evidence that collector biases influenced our re-  
338    sults. Collector random effects were consistently small; Fig 4A, and models fit with and without  
339    this random effect provide qualitatively similar results. The identity of individual scorers did  
340    contribute to observed patterns in endophyte prevalence. For example, 3 of the 16 scorers were  
341    more likely than average to assign positive endophyte status, as indicated by 95% credible in-  
342    tervals that do not overlap 0) (Fig 4B). However, this may have been driven by differences in  
343    scorers biases during the seed scoring process, or by unintended spatial clustering of the speci-  
344    mens scored by each scorer. Interpreting our models with the inclusion of the scorer effect thus  
345    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.

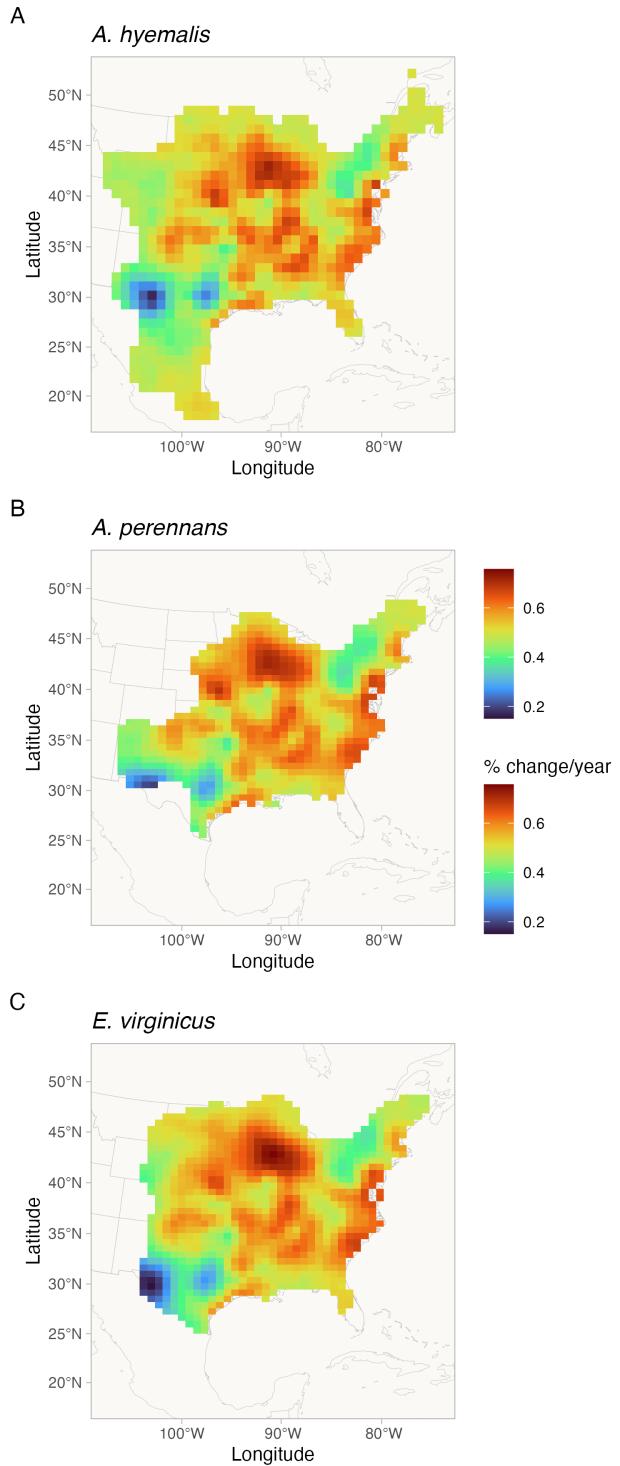


Figure 5: **Mean predicted endophyte prevalence for each host species (columns) in 1925 (top row) and 2020 (bottom row).** Color indicates mean predicted rate of endophyte prevalence across the predicted distribution of each species.

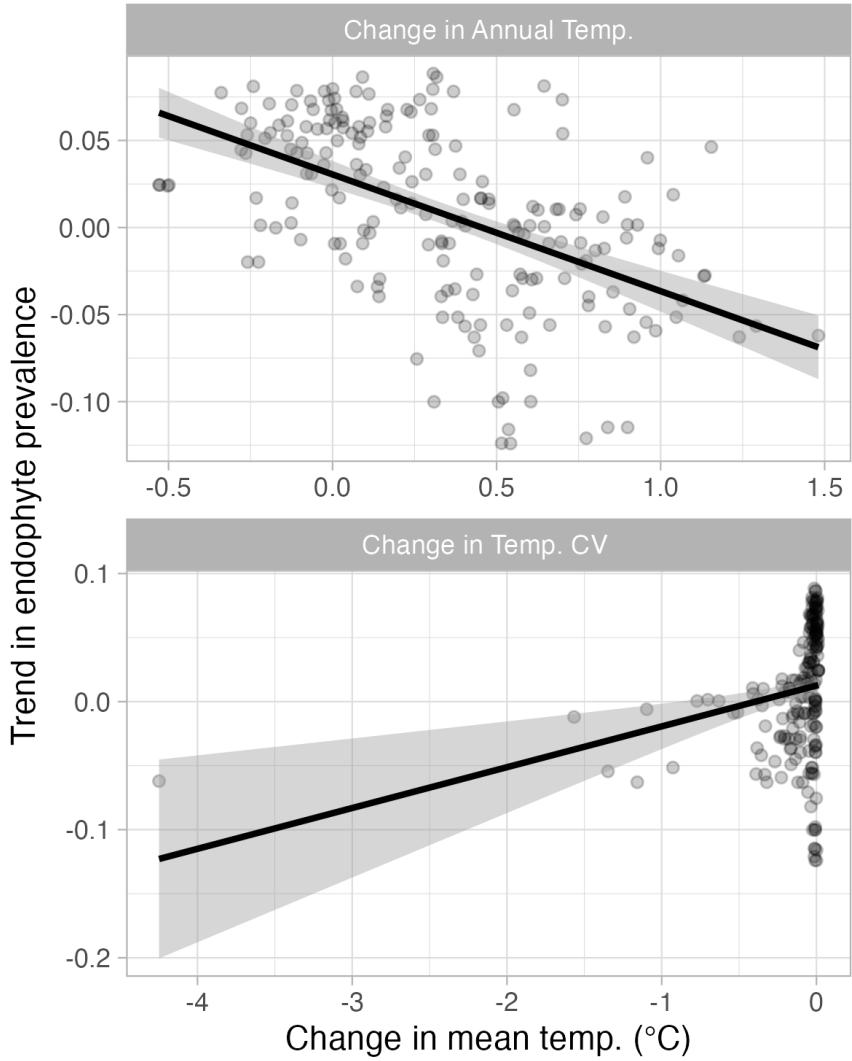
346     What is the relationship between variation in temporal trends in endophyte  
347           prevalence and changes in climate drivers?

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

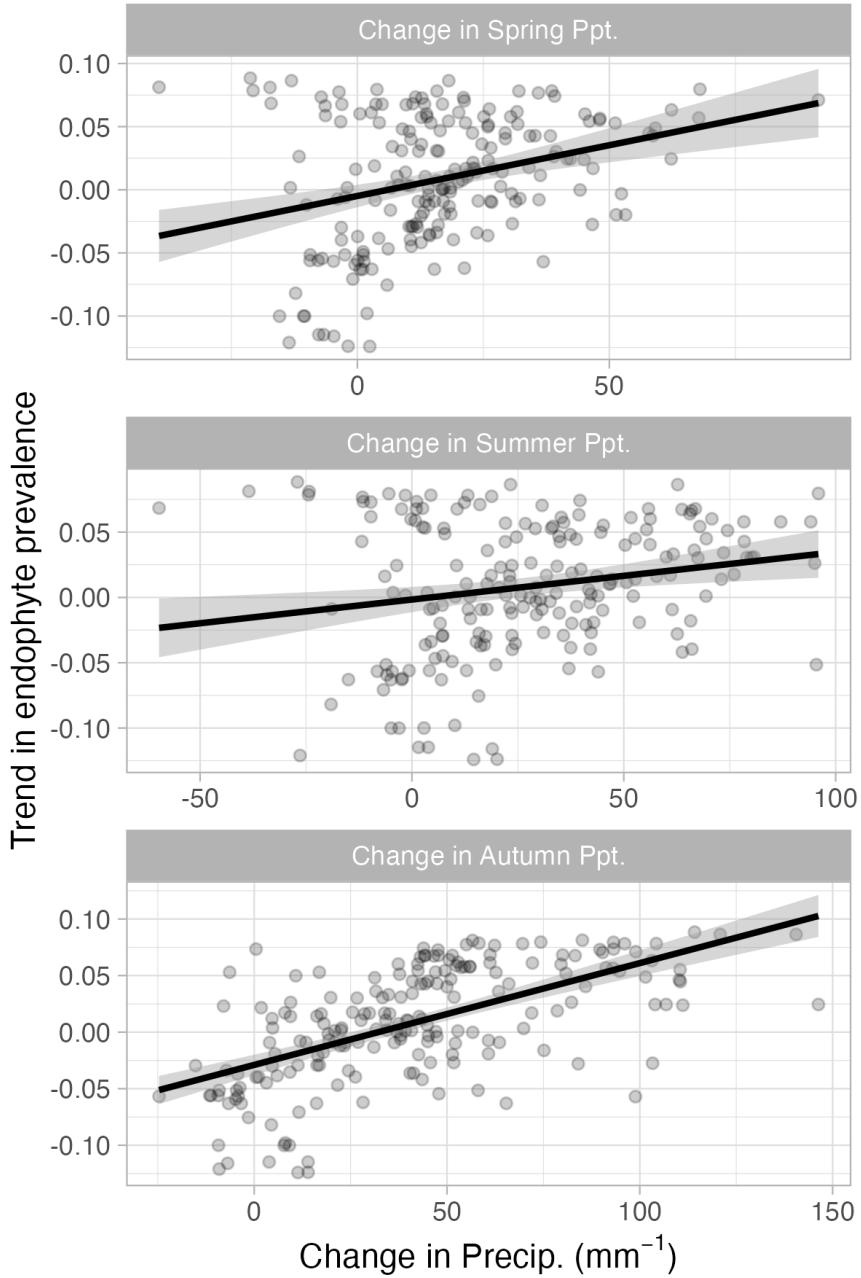
364       26

---

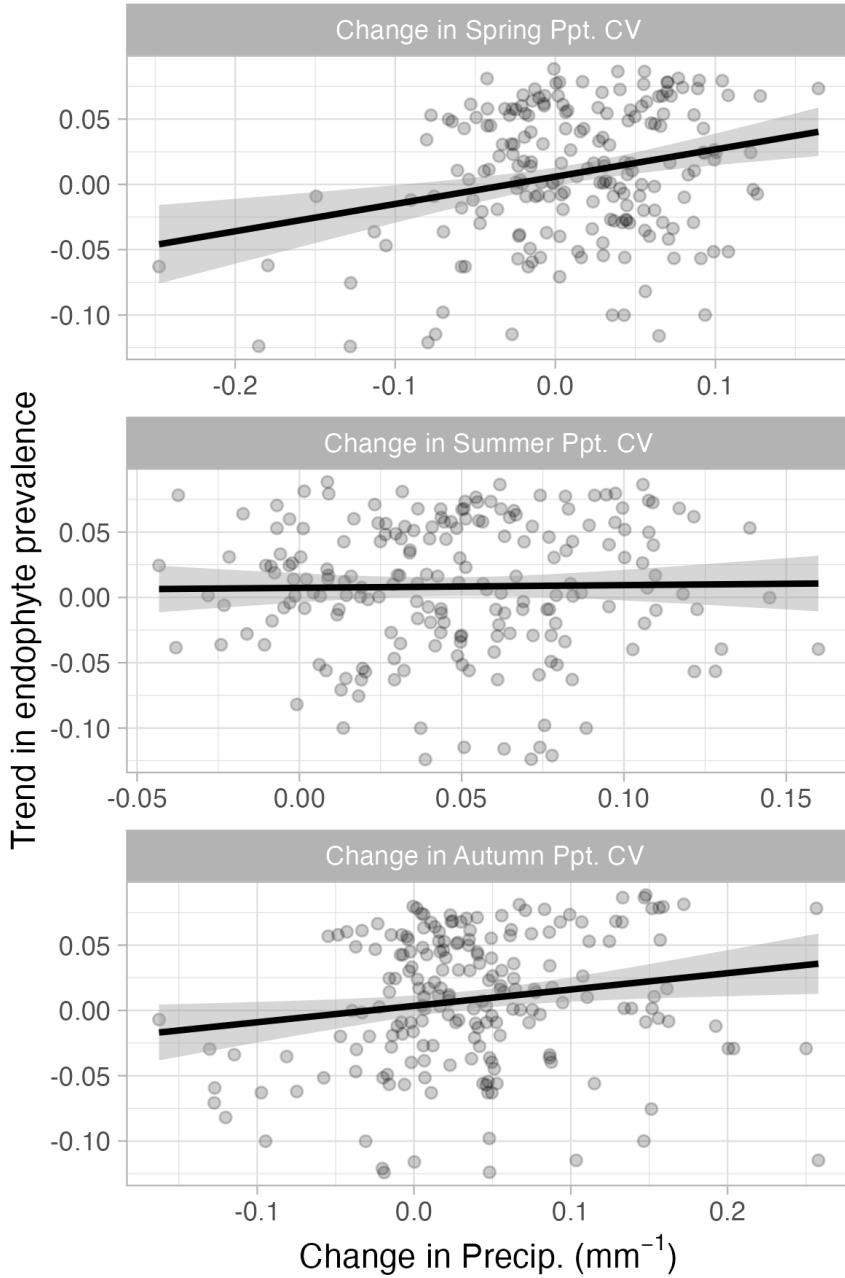
26 Only have plotted results for AGHY right now.



**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  $< -.3$ .

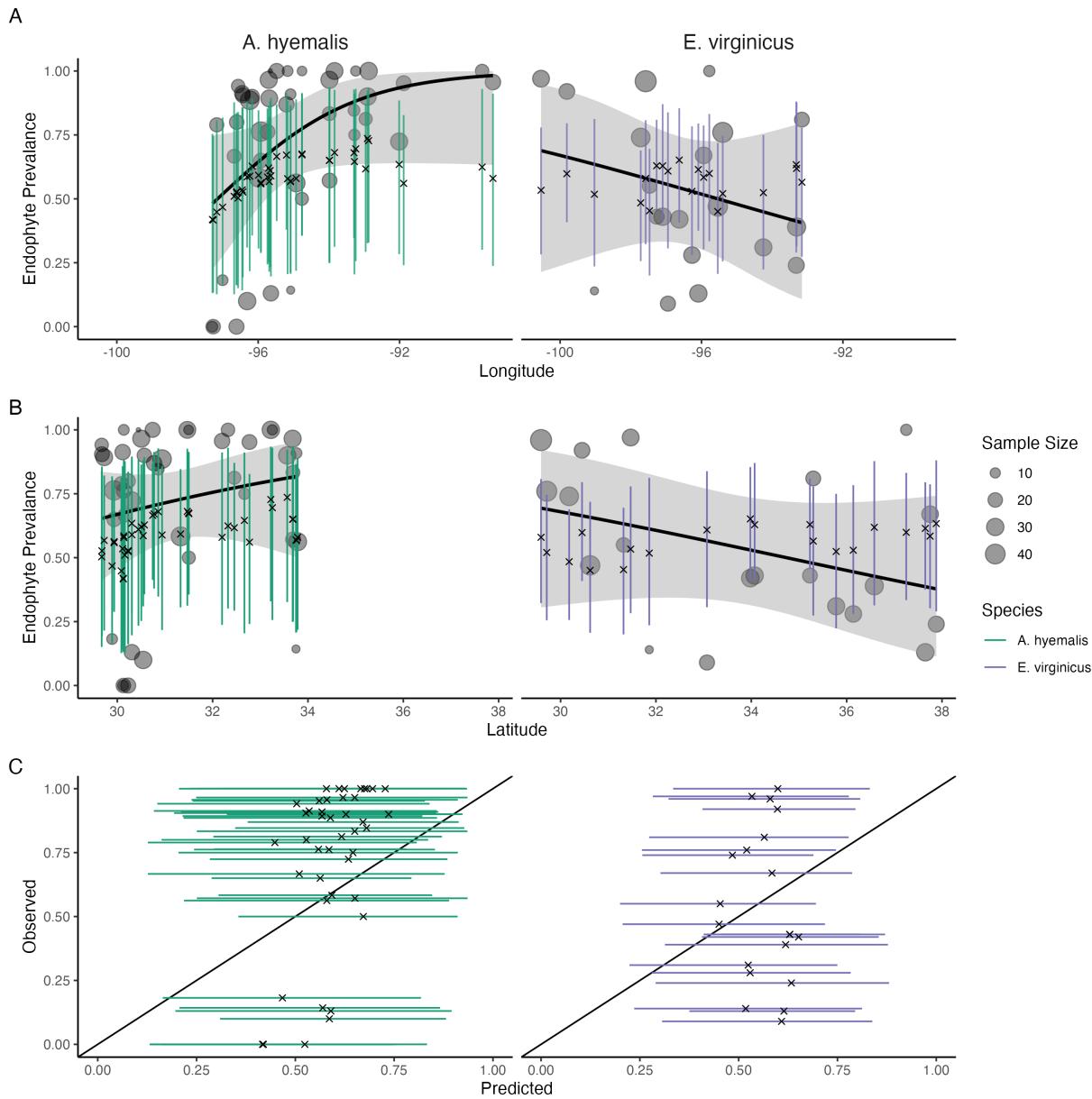


**Figure 8: Correlations between changes in climate drivers and changes in endophyte prevalence.** Color denotes the Spearman correlation coefficient between the relative rate of change in endophyte prevalence and the change in annual mean temperature ( $^{\circ}\text{C}$ ) and total annual and seasonal 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  $< -.3$ .

*365 Performance on test data*

*366 We found that while the model predicts broader regional trends in endophyte prevalence present*  
*367 in the contemporary survey data such as declining endophyte prevalence towards western longi-*  
*368 tudes in *A. hyemalis* (Fig. 9 B-C), however the contemporary data contains additional variability*  
*369 at smaller scales not captured by our sampling of herbarium specimens. We interpreted this to*  
*370 mean that the model captured regional spatial dynamics, but underpredicts local scale dynamics.*

*371 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 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.

## Discussion

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

383 Differences between the responses of each host species underscore that while all of these  
384 C<sub>3</sub> grasses share similar broad-scale distributions, each engages in unique biotic interactions  
385 and has unique niche requirements. We identified hotspots of change for *A. perennans*, which  
386 experienced the strongest absolute changes in endophyte prevalence (Fig. 5). Declines in the  
387 southern portion of its range and increases in the north suggest a potential poleward range shift  
388 of endophytic plants. Based on previous work demonstrating that endophytes can shield their  
389 hosts from drought stress (Decunta et al., 2021), we generally predicted that drought conditions  
390 could be a driver of increasing endophyte prevalence. In line with this expectation, increas-  
391 ing prevalence for this species was associated with decreasing precipitation, most strongly with  
392 autumn-season declines (Fig. 7). *A. perennans* typically blooms in the autumn. Endophytes could  
393 be playing a role helping hosts weather autumn-season droughts while the species is dormant.  
394 It may be useful to investigate whether lagged climate effects are important predictors of host  
395 fitness in this system (Evers et al., 2021). To our knowledge, the response of the symbiosis in  
396 *A. perennans* to drought has not been examined experimentally, but in a greenhouse experiment,  
397 endophytes had a positive effect on host reproduction under shaded, low-light conditions (Davitt

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

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

425 Using test data to validate our model predictions allows us to evaluate places to improve the  
426 model's ability to perform well at out-of-sample prediction, which will be particularly important  
427 for predicting host and symbiont niche-shifts under future climate change. Lack of information  
428 on local variability may simply be a feature of data derived from herbarium specimens. Even  
429 though they are samples from local populations, they are single specimens that are aggregated  
430 over in broad-scale model estimates. Poor predictive ability at local scales in this grass-endophyte  
431 system is not surprising, as previous studies have found that local variation, even to the scale of  
432 hundreds of meters can structure endophyte-host niches (Kazenel et al., 2015). Sneck et al. (2017)  
433 also identified host genotype as an important predictor of endophyte prevalence in *E. virginicus*.  
434 Other studies have found factors including land-use history (Vikuk et al., 2019) and the biotic  
435 environment, including herbivory (Rudgers et al., 2016), to be important predictors of endophyte  
436 ecology. Incorporating available climatic and soil layers as covariates is an obvious first step  
437 that could improve predictions. Towards the goal of predicting the dynamics of microbial sym-  
438 bioses under climate change, models that integrate data from local and regional scales would be  
439 an important step to bridge the gap that often exists between large but broad bioclimatic and  
440 biodiversity data and small but local data on biotic interactions (Isaac et al., 2020; Miller et al.,  
441 2019).

442 Our analysis advances the use of herbarium specimens in global change biology in two ways.  
443 First and foremost, this is the first study to link long-term changes in microbial symbioses to  
444 changes in climate using specimens from natural history collections. The responses of micro-  
445 bial symbioses are a rich target for future studies within museum specimens, particularly those  
446 that take advantage of advances in sequencing technology. While we used relatively coarse  
447 presence/absence data based on fungal morphology, other studies have examined historic plant  
448 microbiomes using molecular sequencing and sophisticated bioinformatics techniques, but these  
449 studies have so far been limited to relatively few specimens at limited spatial extents (Bieker  
450 et al., 2020; Bradshaw et al., 2021; Gross et al., 2021; Heberling and Burke, 2019; Yoshida et al.,  
451 2015). Continued advances in capturing historic DNA and in filtering out potential contami-

452 nation during specimen storage (Bakker et al., 2020; Daru et al., 2019; Raxworthy and Smith,  
453 2021) will be imperative in the effort to scale up these efforts. This scaling up will be essential  
454 to be able to quantify changes not just in the prevalence of symbionts, but also in symbionts'  
455 intraspecific variation and evolutionary responses to climate change, as well as in changes in the  
456 wider microbial community. Answering these questions as well as the unknown questions that  
457 future researchers may ask also reiterates the value in capturing meta-information during ongo-  
458 ing digitization efforts at herbaria around the world and during the accession of newly collected  
459 specimens (Lendemer et al., 2020). Second, we accounted for several potential biases in the data  
460 observation process that may be common to many collections-based research questions by using  
461 a spatially-explicit random effects model. Spatial autocorrelation (Willems et al., 2022), potential  
462 biases introduced by the sampling habits of collectors (Daru et al., 2018), and variation between  
463 contemporary researchers during the collection of trait data, if not corrected for could lead to  
464 over-confident inference about the strength and direction of historic change. Previous studies  
465 that have quantified the effects of collector biases typically find them to be small (Davis et al.,  
466 2015; Meineke et al., 2019), and we similarly did not find that collector has a strong effect on the  
467 results of our analysis. Fitting this model in a Bayesian framework allows for full propagation of  
468 uncertainty.

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

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

## 489 Acknowledgments

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

## 498 Statement of Authorship

## 499 Data and Code Availability

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

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

504

## Appendix A

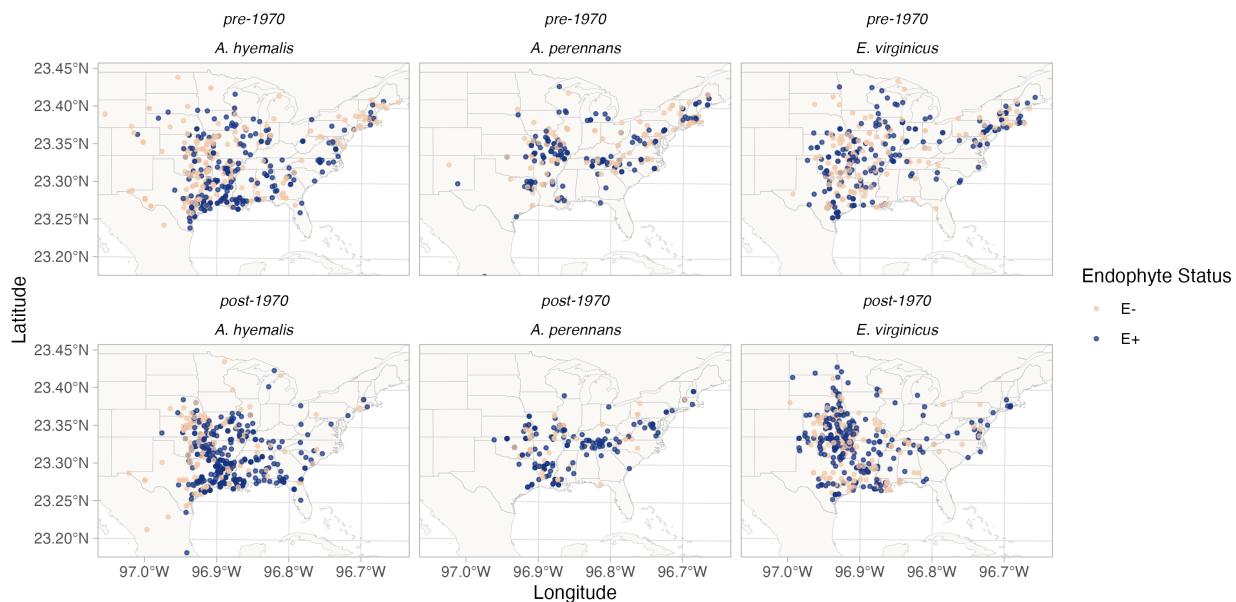
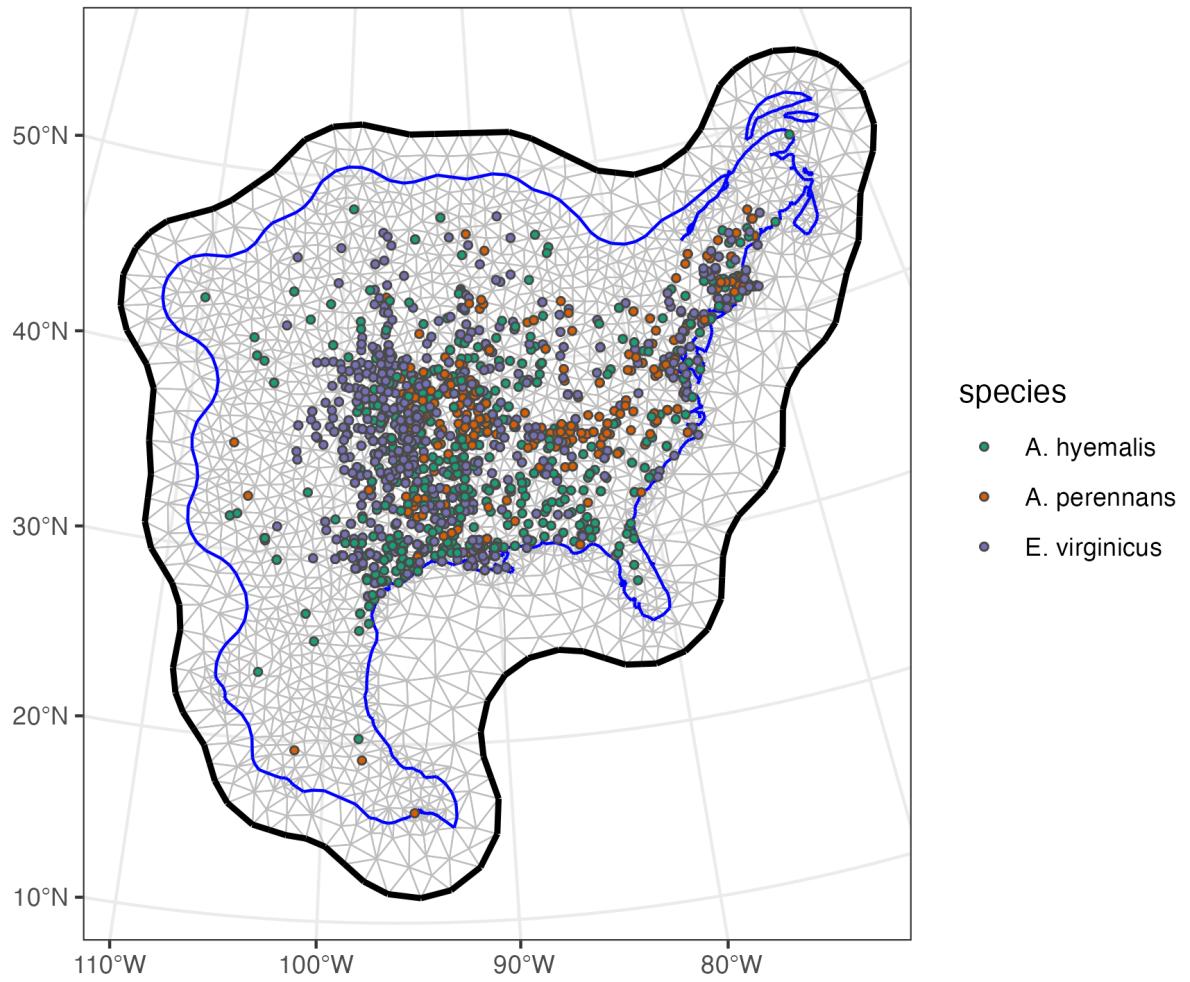
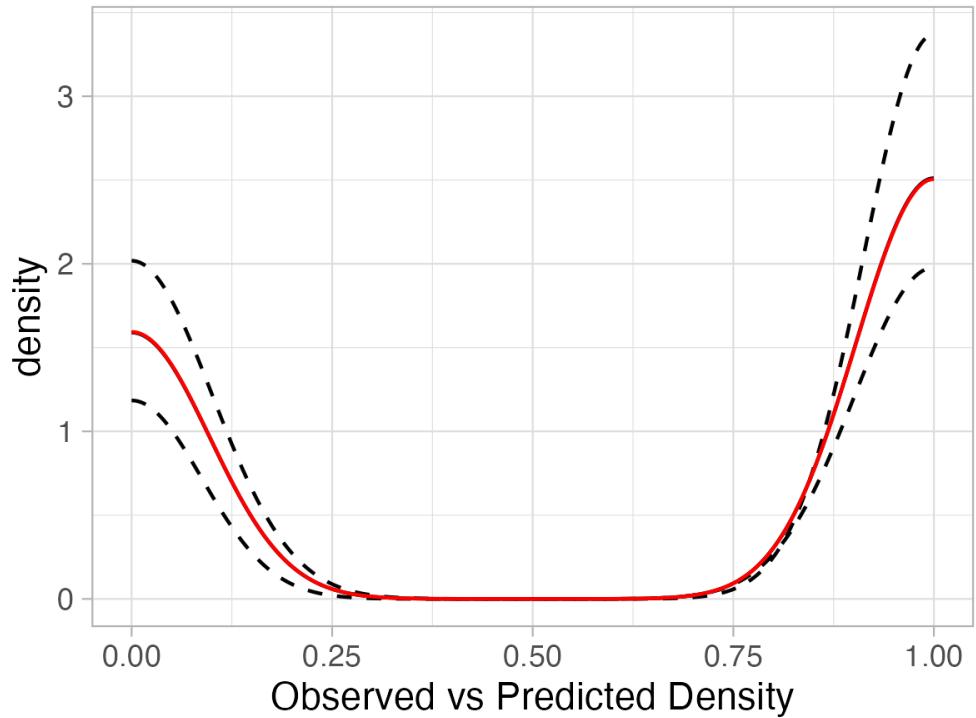


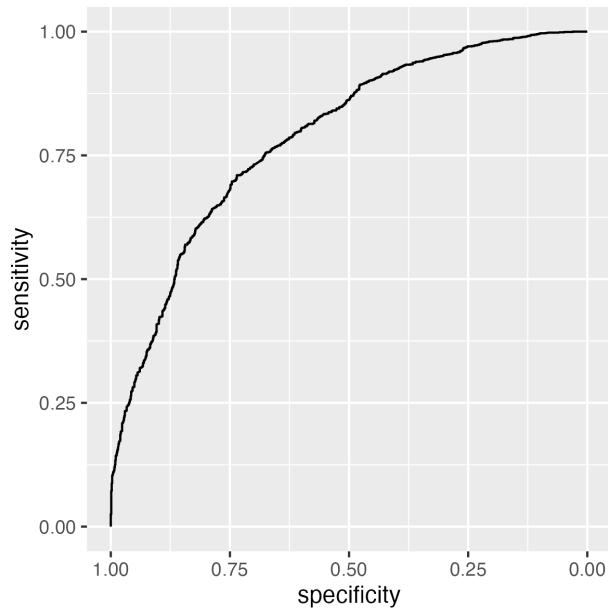
Figure A1: **Endophyte presence/absence in specimens of each host species.** Points show collection locations colored according to whether the specimen contained endophytes ( E+; blue points) or did not contain endophytes (E-, tan points) and are faceted based on collection period.



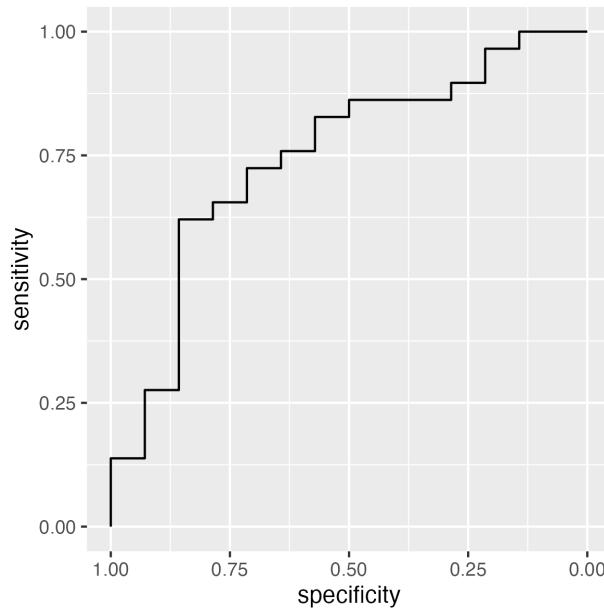
**Figure A2: Triangulation mesh used to estimate spatial dependence between data points.** Grey lines indicate edges of triangles used to define distances between observations. Colored points indicate locations of sampled herbarium specimens for each host species, and the blue line shows the convex hull 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 0.77.



**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.

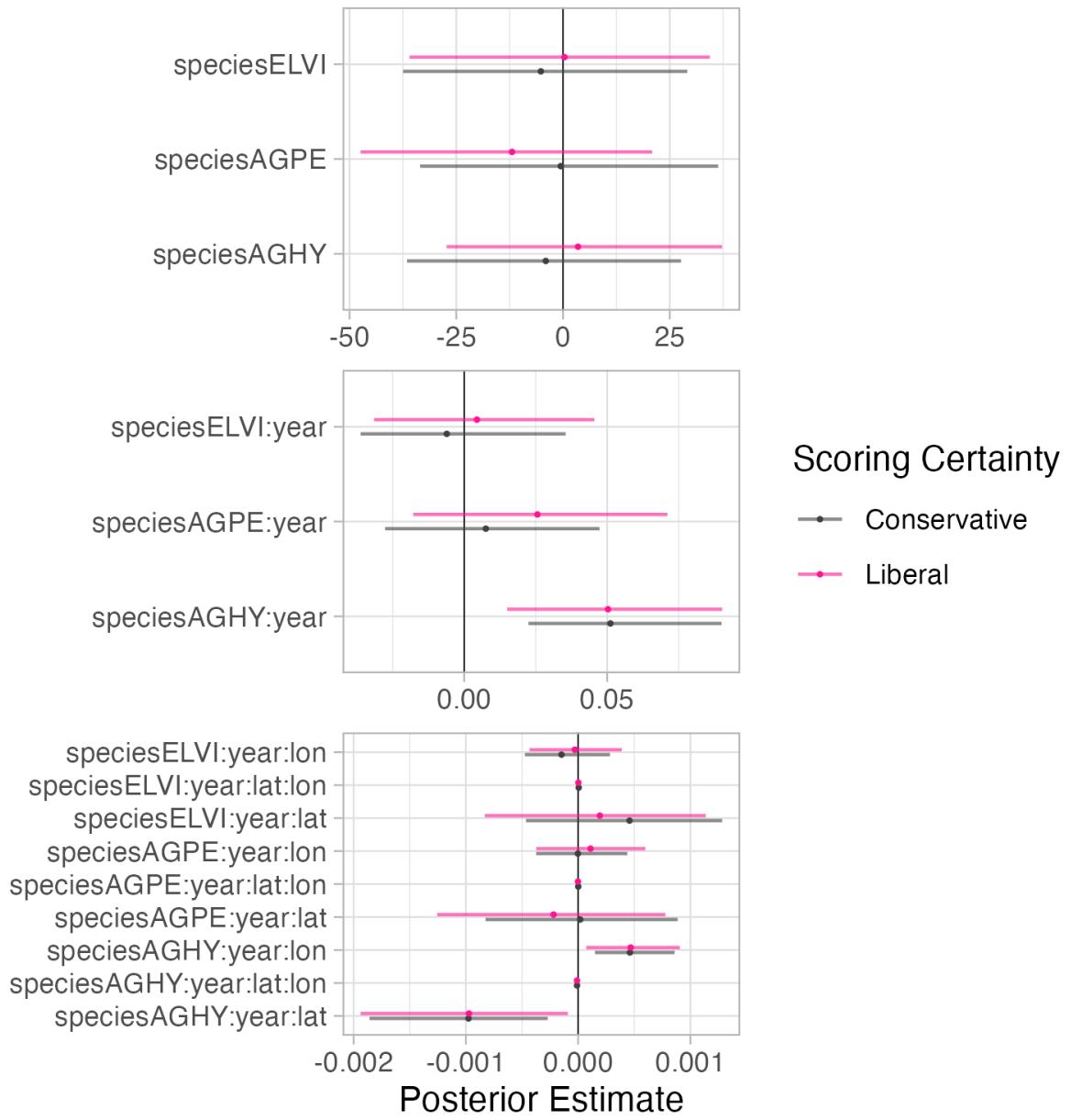


Figure A6: Comparison of posterior estimates of fixed effects when using Liberal or Conservative endophyte scores.

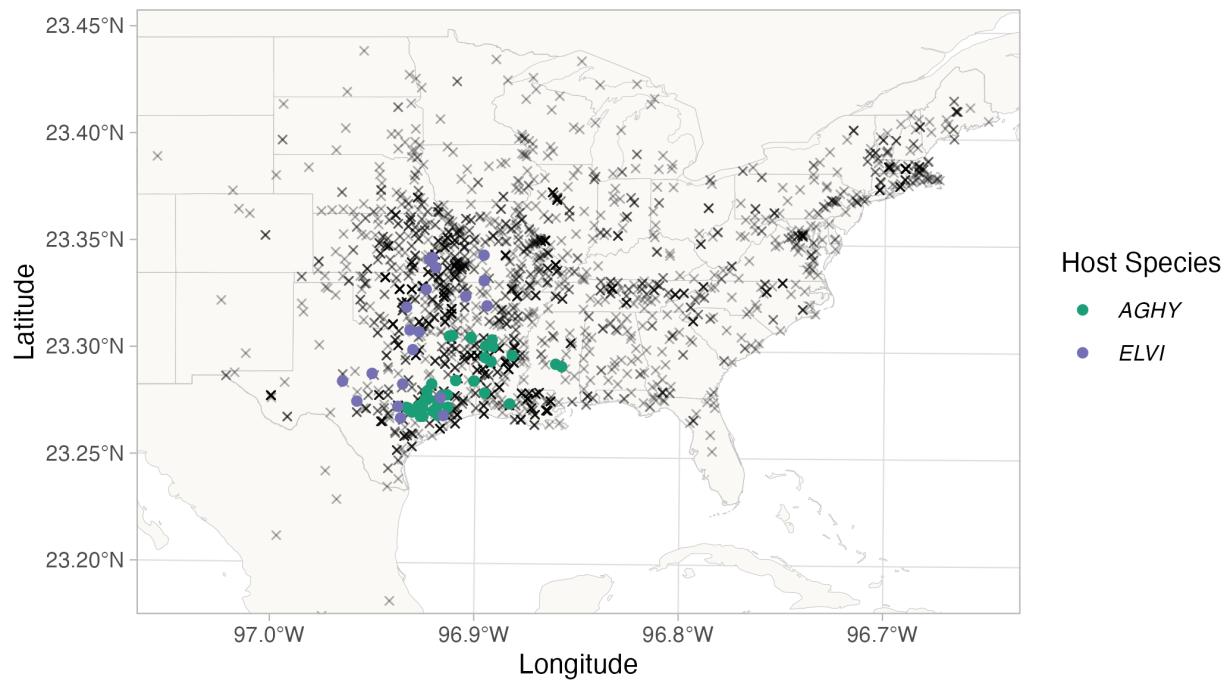
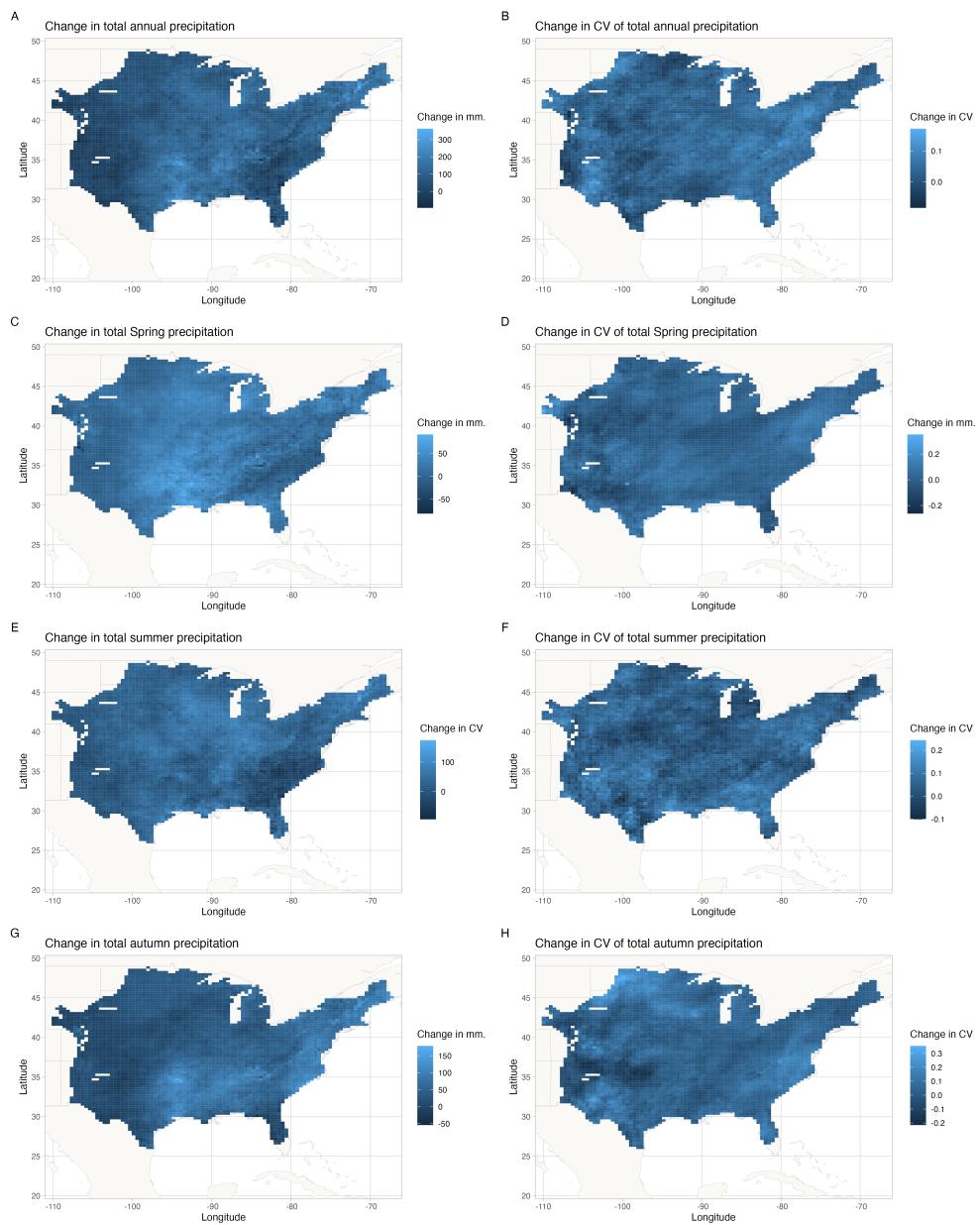
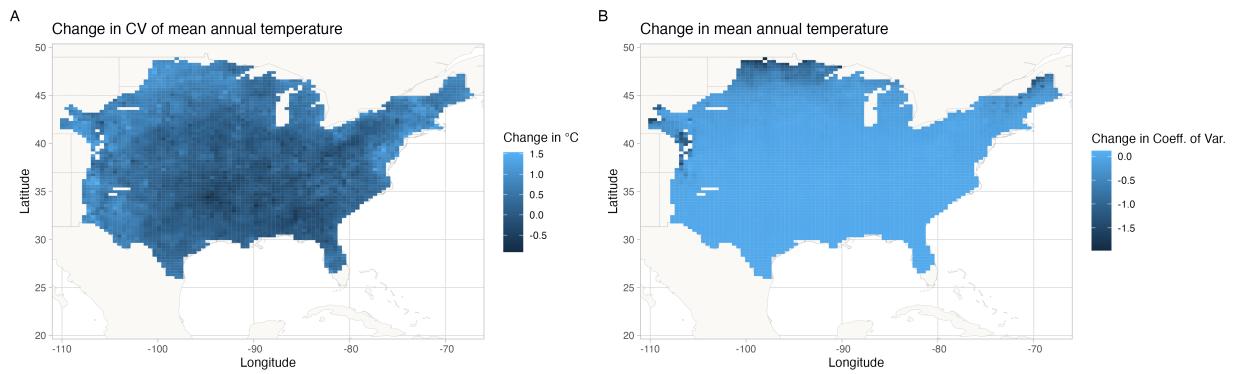


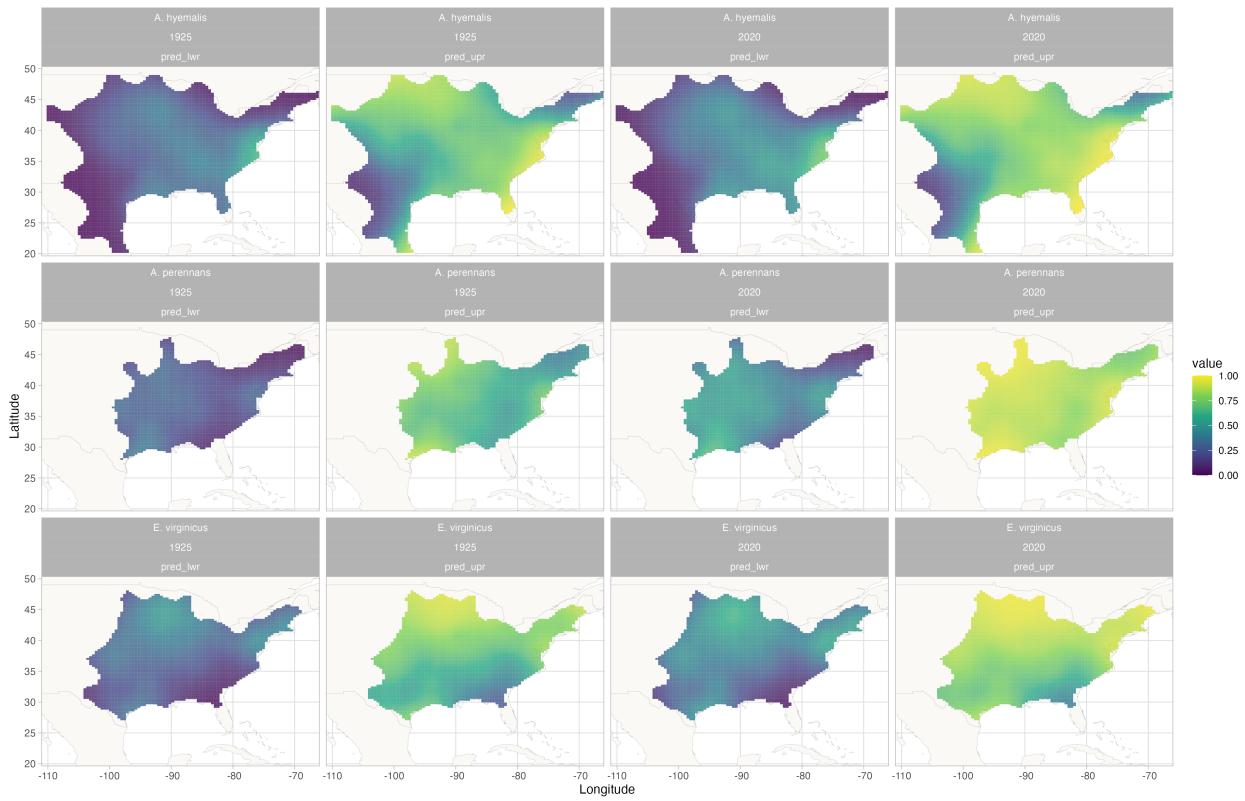
Figure A7: Locations of contemporary surveys of endophytes in *A. hyemalis* used as "test" data (red points), relative to the historical collection data (black crosses).



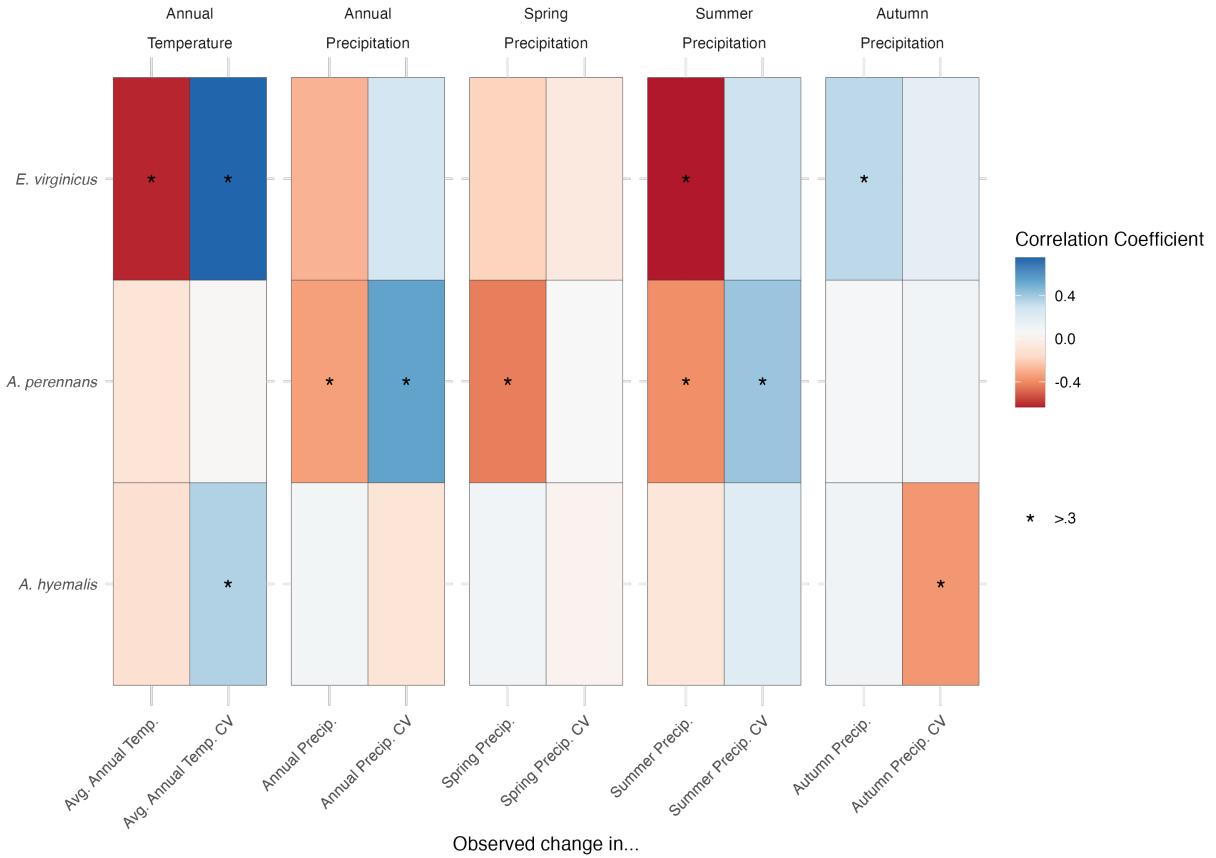
**Figure A8: Change in precipitation between the periods 1895-1925 and 1990-2020.** Color represents change in annual or seasonal total precipitation (A,C,E,G) and in the coefficient of variation of annual or seasonal total precipitation (B,D,F,H). Maps show the study area of *A. hyemalis*. Map pixels used in correlation analysis with endophyte change were pulled from studies areas specific to each host species.



**Figure A9: 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 A10: 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 A11: 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

## 505 Literature Cited

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

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

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

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

- 587 AE Douglas. Host benefit and the evolution of specialization in symbiosis. *Heredity*, 81(6):599–  
588 603, 1998.
- 589 Yuan-Wen Duan, Haibao Ren, Tao Li, Lin-Lin Wang, Zhi-Qiang Zhang, Yan-Li Tu, and Yong-Ping  
590 Yang. A century of pollination success revealed by herbarium specimens of seed pods. *New*  
591 *Phytologist*, 224(4):1512–1517, 2019.
- 592 Markus Engel, Tobias Mette, and Wolfgang Falk. Spatial species distribution models: Using  
593 bayes inference with inla and spde to improve the tree species choice for important european  
594 tree species. *Forest Ecology and Management*, 507:119983, 2022.
- 595 Sanne M Evers, Tiffany M Knight, David W Inouye, Tom EX Miller, Roberto Salguero-Gómez,  
596 Amy M Iler, and Aldo Compagnoni. Lagged and dormant season climate better predict plant  
597 vital rates than climate during the growing season. *Global Change Biology*, 27(9):1927–1941,  
598 2021.
- 599 Paul EM Fine. Vectors and vertical transmission: an epidemiologic perspective. *Annals of the New*  
600 *York Academy of Sciences*, 266(1):173–194, 1975.
- 601 Joshua C Fowler, Shaun Ziegler, Kenneth D Whitney, Jennifer A Rudgers, and Tom EX Miller.  
602 Microbial symbionts buffer hosts from the demographic costs of environmental stochasticity.  
603 *Ecology Letters*, 27(5):e14438, 2024.
- 604 PR Frade, F De Jongh, F Vermeulen, J Van Bleijswijk, and RPM Bak. Variation in symbiont  
605 distribution between closely related coral species over large depth ranges. *Molecular Ecology*,  
606 17(2):691–703, 2008.
- 607 Sarah E Gilman, Mark C Urban, Joshua Tewksbury, George W Gilchrist, and Robert D Holt. A  
608 framework for community interactions under climate change. *Trends in ecology & evolution*, 25  
609 (6):325–331, 2010.

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

- 633 integration for large-scale models of species distributions. *Trends in ecology & evolution*, 35(1):  
634 56–67, 2020.
- 635 Alberto Jiménez-Valverde. Insights into the area under the receiver operating characteristic curve  
636 (auc) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeog-*  
637 *raphy*, 21(4):498–507, 2012.
- 638 David Kahle, Hadley Wickham, and Maintainer David Kahle. Package ‘ggmap’. *Retrieved Septem-*  
639 *ber*, 5:2021, 2019.
- 640 Melanie R Kazenel, Catherine L Debban, Luciana Ranelli, Will Q Hendricks, Y Anny Chung,  
641 Thomas H Pendergast IV, Nikki D Charlton, Carolyn A Young, and Jennifer A Rudgers. A  
642 mutualistic endophyte alters the niche dimensions of its host plant. *AoB plants*, 7:plv005, 2015.
- 643 Roland A Knapp, Gary M Fellers, Patrick M Kleeman, David AW Miller, Vance T Vredenburg,  
644 Erica Bree Rosenblum, and Cheryl J Briggs. Large-scale recovery of an endangered amphibian  
645 despite ongoing exposure to multiple stressors. *Proceedings of the National Academy of Sciences*,  
646 113(42):11889–11894, 2016.
- 647 Mikhail V Kozlov, Irina V Sokolova, Vitali Zverev, Alexander A Egorov, Mikhail Y Goncharov,  
648 and Elena L Zvereva. Biases in estimation of insect herbivory from herbarium specimens.  
649 *Scientific Reports*, 10(1):12298, 2020.
- 650 Benjamin R Lee, Evelyn F Alecrim, Tara K Miller, Jessica RK Forrest, J Mason Heberling,  
651 Richard B Primack, and Risa D Sargent. Phenological mismatch between trees and wildflow-  
652 ers: Reconciling divergent findings in two recent analyses. *Journal of Ecology*, 112(6):1184–1199,  
653 2024.
- 654 James Lendemer, Barbara Thiers, Anna K Monfils, Jennifer Zaspel, Elizabeth R Ellwood, Andrew  
655 Bentley, Katherine LeVan, John Bates, David Jennings, Dori Contreras, et al. The extended  
656 specimen network: A strategy to enhance us biodiversity collections, promote research and  
657 education. *BioScience*, 70(1):23–30, 2020.

- 658 A Leuchtmann. Systematics, distribution, and host specificity of grass endophytes. *Natural toxins*,  
659 1(3):150–162, 1992.
- 660 Adrian Leuchtmann, Charles W Bacon, Christopher L Schardl, James F White Jr, and Mariusz  
661 Tadych. Nomenclatural realignment of neotyphodium species with genus epichloë. *Mycologia*,  
662 106(2):202–215, 2014.
- 663 Finn Lindgren, Håvard Rue, and Johan Lindström. An explicit link between gaussian fields and  
664 gaussian markov random fields: the stochastic partial differential equation approach. *Journal  
665 of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(4):423–498, 2011.
- 666 Canran Liu, Pam M Berry, Terence P Dawson, and Richard G Pearson. Selecting thresholds of  
667 occurrence in the prediction of species distributions. *Ecography*, 28(3):385–393, 2005.
- 668 Margaret McFall-Ngai, Michael G Hadfield, Thomas CG Bosch, Hannah V Carey, Tomislav  
669 Domazet-Lošo, Angela E Douglas, Nicole Dubilier, Gerard Eberl, Tadashi Fukami, Scott F  
670 Gilbert, et al. Animals in a bacterial world, a new imperative for the life sciences. *Proceedings  
671 of the National Academy of Sciences*, 110(9):3229–3236, 2013.
- 672 Timothy D Meehan, Nicole L Michel, and Håvard Rue. Spatial modeling of audubon christmas  
673 bird counts reveals fine-scale patterns and drivers of relative abundance trends. *Ecosphere*, 10  
674 (4):e02707, 2019.
- 675 Emily K Meineke, Charles C Davis, and T Jonathan Davies. The unrealized potential of herbaria  
676 for global change biology. *Ecological Monographs*, 88(4):505–525, 2018.
- 677 Emily K Meineke, Aimée T Classen, Nathan J Sanders, and T Jonathan Davies. Herbarium  
678 specimens reveal increasing herbivory over the past century. *Journal of Ecology*, 107(1):105–117,  
679 2019.
- 680 Abigail R Meyer, Maria Valentin, Laima Liulevicius, Tami R McDonald, Matthew P Nelsen, Jean

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

- 704 François Renoz, Inès Pons, and Thierry Hance. Evolutionary responses of mutualistic insect–  
705 bacterial symbioses in a world of fluctuating temperatures. *Current opinion in insect science*, 35:  
706 20–26, 2019.
- 707 Elizabeth Lewis Roberts and Aileen Ferraro. Rhizosphere microbiome selection by epichloë en-  
708 dophytes of *festuca arundinacea*. *Plant and soil*, 396:229–239, 2015.
- 709 RJ Rodriguez, JF White Jr, Anne E Arnold, and a RS and Redman. Fungal endophytes: diversity  
710 and functional roles. *New phytologist*, 182(2):314–330, 2009.
- 711 Gregor Rolshausen, Francesco Dal Grande, Anna D Sadowska-Deś, Jürgen Otte, and Imke  
712 Schmitt. Quantifying the climatic niche of symbiont partners in a lichen symbiosis indicates  
713 mutualist-mediated niche expansions. *Ecography*, 41(8):1380–1392, 2018.
- 714 Jennifer A Rudgers and Angela L Swafford. Benefits of a fungal endophyte in *elymus virginicus*  
715 decline under drought stress. *Basic and Applied Ecology*, 10(1):43–51, 2009.
- 716 Jennifer A Rudgers, Michelle E Afkhami, Megan A Rúa, Andrew J Davitt, Samantha Hammer,  
717 and Valérie M Huguet. A fungus among us: broad patterns of endophyte distribution in the  
718 grasses. *Ecology*, 90(6):1531–1539, 2009.
- 719 Jennifer A Rudgers, Rebecca A Fletcher, Eric Olivas, Carolyn A Young, Nikki D Charlton, Dean E  
720 Pearson, and John L Maron. Long-term ungulate exclusion reduces fungal symbiont prevalence  
721 in native grasslands. *Oecologia*, 181:1151–1161, 2016.
- 722 Håvard Rue, Sara Martino, and Nicolas Chopin. Approximate bayesian inference for latent gaus-  
723 sian models by using integrated nested laplace approximations. *Journal of the royal statistical  
724 society: Series b (statistical methodology)*, 71(2):319–392, 2009.
- 725 Kari Saikkonen, Pedro E Gundel, and Marjo Helander. Chemical ecology mediated by fungal  
726 endophytes in grasses. *Journal of chemical ecology*, 39:962–968, 2013.

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

- 751 Veronika Vikuk, Carolyn A Young, Stephen T Lee, Padmaja Nagabhyru, Markus Krischke, Mar-  
752 tin J Mueller, and Jochen Krauss. Infection rates and alkaloid patterns of different grass species  
753 with systemic epichloë endophytes. *Applied and Environmental Microbiology*, 85(17):e00465–19,  
754 2019.
- 755 Zhengfeng Wang, Chunjie Li, and James White. Effects of epichloë endophyte infection on  
756 growth, physiological properties and seed germination of wild barley under saline conditions.  
757 *Journal of Agronomy and Crop Science*, 206(1):43–51, 2020.
- 758 Robert J Warren and Mark A Bradford. Mutualism fails when climate response differs between  
759 interacting species. *Global Change Biology*, 20(2):466–474, 2014.
- 760 Nicole S Webster, Rose E Cobb, and Andrew P Negri. Temperature thresholds for bacterial  
761 symbiosis with a sponge. *The ISME journal*, 2(8):830–842, 2008.
- 762 James F White and Garry T Cole. Endophyte-host associations in forage grasses. i. distribution  
763 of fungal endophytes in some species of lolium and festuca. *Mycologia*, 77(2):323–327, 1985.
- 764 Franziska M Willems, JF Scheepens, and Oliver Bossdorf. Forest wildflowers bloom earlier as  
765 europe warms: lessons from herbaria and spatial modelling. *New Phytologist*, 235(1):52–65,  
766 2022.
- 767 Charles G Willis, Elizabeth R Ellwood, Richard B Primack, Charles C Davis, Katelin D Pearson,  
768 Amanda S Gallinat, Jenn M Yost, Gil Nelson, Susan J Mazer, Natalie L Rossington, et al. Old  
769 plants, new tricks: Phenological research using herbarium specimens. *Trends in ecology &*  
770 *evolution*, 32(7):531–546, 2017.
- 771 Chao Xia, Nana Li, Yawen Zhang, Chunjie Li, Xingxu Zhang, and Zhibiao Nan. Role of epichloë  
772 endophytes in defense responses of cool-season grasses to pathogens: A review. *Plant disease*,  
773 102(11):2061–2073, 2018.
- 774 Kentaro Yoshida, Eriko Sasaki, and Sophien Kamoun. Computational analyses of ancient

<sup>775</sup> pathogen dna from herbarium samples: challenges and prospects. *Frontiers in plant science*,

<sup>776</sup> 6:771, 2015.