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Climate change and plant-microbe interactions: Water-availability influences the effective specialization of a fungal pathogen

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ABSTRACT

Through species-specific effects on plants, pathogens play a key role in structuring plant communities. A change in abiotic context, such as those mediated by climate change, may alter plant communities through changes in the specificity of plant-pathogen interactions. To test how water availability influenced the specificity of plant-pathogen interactions, we grew paired congeners of three native and three nonnative coastal prairie plant species with or without a pathogenic soil fungus, *Fusarium incarnatum-equiseti* species complex 6 b, under low, average, and high water treatments. Across the plant species tested, the *Fusarium* treatment had stronger negative and species-specific effects on plant biomass at high water availability than low water availability. If generalizable, our results suggest that stronger and more species-specific pathogen effects could drive changes in plant community composition in wetter conditions, but plant-pathogen interactions may be less important for plant community structure in drier conditions.

1. Introduction

Global climate change, characterized by shifts in climatic regimes and rising extreme weather events, continues to disrupt and shape biotic interactions (Blois et al., 2013; Cahill et al., 2013; Rudgers et al., 2020; Trivedi et al., 2022). Under anthropogenic climate change, flooding and drought have become more frequent and severe, altering the ranges, diversity, composition, and productivity of plant communities (Parmesan and Hanley, 2015; Hudson et al., 2022). Precipitation patterns will continue to change. Globally, precipitation will increase, but droughts are expected to become more severe with increased atmospheric evaporative demand (Easterling et al., 2017). How plant communities will respond to ongoing changes in water availability and other abiotic conditions will likely depend on their symbiotic associations with belowground microbial communities (Classen et al., 2015; Rudgers et al., 2020). Microbial mutualists, such as arbuscular mycorrhizal fungi, may help buffer plants against water stresses (Auge, 2001) while pathogens may become more abundant or more effective depending on abiotic context (van der Putten et al., 2016).

Plant pathogens may have particularly important consequences for ecosystems, especially under climate change. As environmental conditions continue to shift, the emergence of parasitic microorganisms is expected (Fones et al., 2017). Increasing annual precipitation levels in the Great Plains, Midwestern, and Northeastern regions of the United States, coupled with rising temperatures, are likely to benefit pathogens that thrive under such conditions (Easterling et al., 2000). Simultaneously, climatic selection pressures may drive evolutionary changes that lead to host range expansion, and climate effects on host range and host susceptibility could contribute to the proliferation of outbreaks (Shaw and Osborne, 2011). For example, following a major storm event on the Texas coast, the rust fungus *Coleosporium solidaginis* was identified on a new host, *Liatris pycnostachya* (Luecke and Crawford, 2019). While pathogen emergence poses a threat to vulnerable hosts, plant pathogens play key roles in coexistence. For example, plant pathogens can promote coexistence by producing negative frequency dependence through plant-soil feedbacks (Bever et al., 2015).

The species specificity of pathogens can determine whether they influence plant community composition (van Ruijven et al., 2020). For example, host-specific enemies are necessary for the generation of plant-soil feedbacks and the maintenance of diversity through Janzen-Connell effects (Benítez et al., 2013; Bever et al., 2015). Conversely, when microbes equally affect plants (i.e., they have no

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species specificity), they are not expected to influence plant community structure. Even though there is evidence that most pathogenic fungi may be generalists, they often exert species-specific effects on their host plants, creating "effective specialization" (Benítez et al., 2013; Sarmiento et al., 2017; Spear and Broders, 2021). However, the extent of effective specialization may depend on the abiotic environment, as environmental conditions can shift plant-pathogen interactions (Hersh et al., 2012; Lin et al., 2012). If a change in abiotic conditions changes the host-specificity of plant-microbe interactions, then it could enhance or diminish the importance of plant-microbe interactions in structuring communities. Critically, this could occur without a change in microbial community composition. For example, if dry conditions weaken the effect of generalist pathogens so they equally affect competing plant species, it could cause the breakdown of a critical coexistence mechanism as plant-soil feedback could shift from coexistence-stabilizing negative feedback to neutral feedback.

Because they lack a history of coadaptation with local pathogens, nonnative plant species may be less affected by pathogens than native species (Callaway et al., 2004). Therefore, they may be spared when abiotic conditions strengthen pathogen effects. In turn, abiotic conditions that increase pathogen suppression of native species may increase the likelihood that nonnative species will become invasive species. For example, the conditions that generally increase pathogen abundance (high water and high temperatures) also favor the presence and abundance of nonnative plant species (Stohlgren et al., 2002). Alternatively, closely related plant species are more likely to share pathogens (Gilbert and Webb 2007; Parker et al., 2015). If relatedness is a stronger predictor of pathogen effect than a history of coadaptation between pathogen and host, then native and nonnative plant species may respond similarly to pathogens.

Here we established a laboratory experiment to determine how water availability and plant host identity influence the effects of a pathogenic soil fungus on congeneric pairs of native and nonnative grassland plant species. Specifically, we addressed the following questions: (i) Does the pathogen display effective specialization? (ii) Does water availability influence the effective specialization of the pathogen? (ii) Does a change in water availability benefit nonnative species through changes in plant-pathogen interactions?

2. Materials and methods

We conducted a lab experiment where we grew 3 plant species native to the Texas coastal prairie (*Bothriochloa barbinodis*, *Paspalum floridanum*, *Verbena xutha*) and 3 nonnative plant species (*Bothriochloa ischaemum*, *Paspalum urvillei*, *Verbena brasiliensis*) in the presence or absence of a pathogenic soil fungi, *Fusarium incarnatum-equiseti* species complex 6 b. We chose these species based on (1) the nonnative species being problematic in the coastal prairie, (2) the nonnative species having a native congener, and (3) seed availability given the timing of the experiment. Seeds for *V. xutha*, *P. floridanum*, and *P. urvillei* were collected from populations in and around Houston, TX, USA. Seeds for *V. brasiliensis* were collected from Baton Rouge, LA, USA. Seeds for *B. barbinodis* were purchased from Native American Seed Company (Junction, TX, USA), which collects seeds from grasslands across Texas, and seeds for *B. ischaemum* were purchased from Turner Seed Company (Breckenridge, TX, USA). The *Fusarium* isolate we used was isolated from the roots of *Andropogon gerardii* that was growing in remnant coastal prairie at the University of Houston Coastal Center (29.39082° N, 95.03354° W). The culture was collected as part of a larger project to evaluate the factors that influence the fungal communities of dominant North American grasses. In the larger survey, this species was also commonly found associated with *Schizachyrium scoparium* at the same site and other sites in North and East Texas. Details on the collection procedures can be found in previous publications (Lagueux et al., 2020; Rudgers et al., 2022). Members of the *Fusarium incarnatum-equiseti* species complex include documented plant pathogens as well as commensal plant endophytes (Summerell, 2019). Some *Fusarium* species that are damaging to crops are harbored asymptomatically in native grasses (Lofgren et al., 2018). In previous work, the isolate we used negatively affected the growth of *Boutelaua gracilis* (J. Rudgers, *unpublished* data). To determine the effect of water availability on the specificity of plant-microbe interactions, we administered three watering treatments simulating drought, ambient rainfall, and flooding conditions based off of 30-year precipitation averages from the Houston area (for additional details, see Dudenhöffer et al., 2022). While we did not measure soil moisture content in this experiment, we used the same sized pots and similar soil and growing conditions as in Dudenhöffer et al. (2022). This, combined with the decrease in plant biomass with decreased water for most plant species gave us confidence that our low watering treatments were stressful for the plants. Each treatment combination was replicated 10 times, for a total of 360 pots (6 plant species × 2 *Fusarium* treatments × 3 watering treatments × 10 replicates).

We grew each plant in conical pots that were approximately 5 cm in diameter and 18 cm deep (Stuewe & Sons, Inc.; Tangent, OR, USA). Pots were assembled by adding 10 cm × 10 cm sterile linen squares to the bottom of the pots to prevent soil from falling through and tightly packing the pots with sterile potting soil (MetroMix 840, Sungro, Agawam, MA, USA) leaving approximately a 2.5 cm gap at the top. To ensure sterility, we covered the assembled pots with aluminum foil and autoclaved them twice at 121 °C for 30 min, with a 24 h resting period in between cycles. To provide a natural background soil community, we pipetted 10 ml of a soil slurry onto the soil surface of each pot. Soil was collected in the coastal prairie at the University of Houston Coastal Center. The slurry was prepared by blending the live field soil in water (50% by volume) and filtering the mixture through a 500 μm sieve. We allowed the background microbial community to establish for 14 days. Then, half of the pots received 10 ml of *Fusarium* inoculum that was prepared by removing and rinsing *Fusarium* hyphae mats growing on 17 100 × 15 mm LB plates and blending them in 3.8 L of DI water. The other pots received 10 ml of DI water as a control.

In preparation for planting, seeds were surface sterilized by soaking in 10% NaClO for 10 min. We also carried out a scarification step by suspending the seeds in a mixture of DI water and sterile sand while stirring for 1 min. Following the application of the *Fusarium* treatment, we added approximately 6 seeds of a single species to each pot. To help with germination success and plant establishment, all pots were watered with 15 ml of DI water every weekday for 8 weeks. Then, plants were thinned to a single individual and we began to apply the watering treatments. All pots were watered three times per week, with the low water treatment pots receiving 5 ml of DI water, the medium water treatment pots receiving 15 ml of DI water, and the high water treatment pots receiving 25 ml of DI water. The pots were fully randomized and suspended in racks (Stuewe & Sons, Inc.; Tangent, OR, USA), which helps prevent movement of microbes among pots from bottom watering. During the duration of the experiment, the plants were grown in an indoor laboratory (approximately 22 °C and 60% humidity) under growth lights (Virtual Sun T5 HO fluorescent lights; Ontario, CA, USA) that remained on for 12 h per day. After 7 weeks of the water treatments, aboveground and belowground biomass was harvested, dried, and weighed. To separate belowground biomass, roots were carefully separated from loose soil. Then, roots were submerged in water to remove more soil and finally washed over a sieve to remove soil stuck to the roots. All plant material was dried in a drying oven at 60 °C.

Statistical analyses. All statistics were performed in R version 4.1.3 (R Core Team, 2022). We tested treatment effects on plant biomass by fitting generalized linear models with the fixed effects of plant species, water treatment, *Fusarium* treatment, and all possible interactions followed by 'Anova' in the car package with Type III sum of squares (Fox and Weisberg, 2019). Biomass values were square root transformed to improve normality of residuals. Results for aboveground, belowground, and total biomass were qualitatively similar (Table S1). Therefore, we focus our results on total biomass. Following a plant species × water

treatment × *Fusarium* interaction with a p-value <0.05, we tested for treatment effects on total biomass within each plant species.

To test whether the water treatments influence the species specificity of the *Fusarium* effect, we tested treatment effects on total biomass within each water treatment. A significant plant species × *Fusarium* effect would indicate species specificity in the response. The *Fusarium* effect size for total biomass was estimated for each treatment combination by fitting a generalized linear model with a log link function and a gaussian distribution. The treatment estimate for *Fusarium* is then equivalent to the log response ratio, i.e., the natural log of the ratio of the mean total biomass with versus without *Fusarium*. A small value (0.0001) was added to the total biomass values to avoid undefined numbers (i.e., natural log of zero). Then, we applied non-parametric bootstrapping to refit the model using 1000 iterations to estimate 95% confidence intervals for the log response ratio ('boot' package; Davison and Hinkley, 1997; Canty and Ripley, 2020). We excluded the treatment combination that had 100% mortality (*Paspalum urvillei* in the low water treatment in the absence of *Fusarium*).

We tested whether nonnative and native species differed in their responses using a mixed effect model with the fixed effects of species

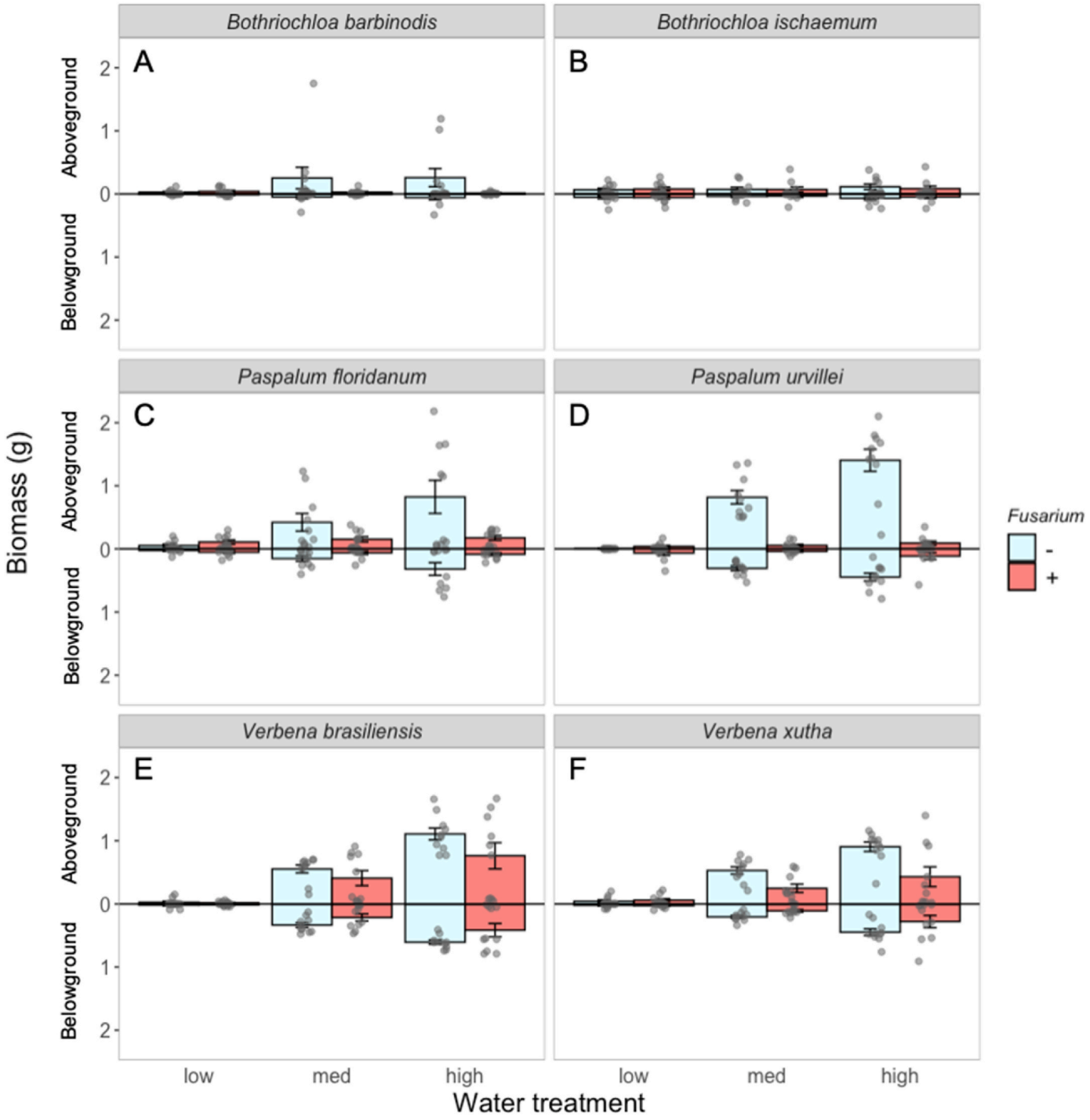

Fig. 1. Effect of the water treatments and *Fusarium* on the biomass of six plant species: *Bothriochloa barbinodis* (A), *Bothriochloa ischaemum* (B), *Paspalum floridanum* (C), *Paspalum urvillei* (D), *Verbena xutha* (E), *Verbena brasiliensis* (F). Bars are average aboveground and belowground biomass with standard errors. Gray points show values for individual plants.

provenance (native or nonnative), water treatment, and *Fusarium* treatment, all possible interactions, and the random effect of species nested in species provenance ('lme4' package; Bates et al., 2015).

Project data is available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.24019725.

3. Results

The effect of the water treatment, the *Fusarium* treatment, and the interaction of the two treatments depended on plant species identity (Table S1). The effect of the treatments on the two *Bothriochloa* species was relatively weak (Fig. 1, Table 1). The native *B. barbinodis* produced 84% less biomass in the presence of *Fusarium* (Fig. 1, Table 1), but its biomass was not significantly affected by the water or the interaction between water and the *Fusarium* treatment. Nonnative *B. ischaemum* was not influenced by water, the *Fusarium* treatment, or their interaction. In contrast, water mediated the effect of the *Fusarium* treatment on the biomass of the two *Paspalum* species (Fig. 1, Table 1). In the low water treatment, the *Fusarium* treatment benefited both *Paspalum* species; the *Fusarium* treatment doubled the biomass of the native *P. floridanum*, and the nonnative *P. urvillei* only survived to harvest when the *Fusarium* was present. However, in the medium and high water treatments, the *Fusarium* treatment decreased the biomass of the native *P. floridanum* by an average of 70% and the biomass of nonnative *P. urvillei* by an average of 90%. The *Fusarium* treatment decreased biomass of the two *Verbena* species, with a 46% decrease in biomass for the nonnative *V. brasiliensis* and a 31% decrease for the native *V. xutha* (Fig. 1, Table 1). However, only *V. brasiliensis* biomass was influenced by an interaction between the water treatment and the *Fusarium* treatment. In the low water treatment, the *Fusarium* treatment increased *V. brasiliensis* biomass by 33%, but decreased *V. brasiliensis* biomass by an average of 49% in the medium and high water treatments (Fig. 1, Table 1).

Within the water treatments, species did not differ in their response to the *Fusarium* treatment in the low water treatment ($F_{5,\ 108} = 1.22$, $P = 0.30$), but did in the medium ($F_{5,\ 108} = 4.52$, $P = 0.0009$) and high ($F_{5,\ 108} = 3.62$, $P = 0.005$) water treatments. In the low water treatments, effect sizes trended positive, but 95% confidence intervals overlapped zero (Fig. 2). In the medium and high water treatments, species were significantly negatively affected by the *Fusarium* treatment and the strength of the effect differed across species (Fig. 2).

Native and nonnative species did not differ in their biomass or their responses to the treatments (Table 2).

Table 1
Results from generalized linear models testing the effects of water treatment, *Fusarium* treatment, and their interactions on total biomass of the six plant species. Nonnative species are denoted by ^. For each species, the numerator and denominator degrees of freedom for the statistical tests were 2, 54 for the water treatment, 1, 54 for the *Fusarium* treatment, and 2, 54 for the interaction. Bold *P*-values are statistically significant at $P < 0.05$.

	Water		*Fusarium*		Water × *Fusarium*	
	F	P	F	P	F	P
Bothriochloa barbinodis	0.8756	0.4224	4.2867	**0.0432**	1.8204	0.1718
Bothriochloa ischaemum^	0.4575	0.6353	0.0658	0.7986	0.0843	0.9192
Paspalum floridanum	7.9105	**0.0010**	4.1976	**0.0454**	3.7823	**0.0290**
Paspalum urvillei^	67.123	< **0.0001**	82.851	< **0.0001**	50.194	< **0.0001**
Verbena xutha	57.2456	< **0.0001**	5.5136	**0.0226**	1.8474	0.1675
Verbena brasiliensis^	40.9705	< **0.0001**	9.9224	**0.0027**	4.8264	**0.0118**

4. Discussion

The effective specialization of pathogens can play an important role in structuring plant communities (Benítez et al., 2013). However, the outcome of biotic interactions can be shaped by the abiotic environment, and the abiotic context-dependency of effective specialization is relatively unexplored (but see Moricca and Ragazzi, 2008; Hersh et al., 2012). We found that water availability shifted the interaction outcome between *Fusarium* and six coastal prairie species from more positive and generalist in the low watering treatment to more species-specific and negative in the high water treatment. Interestingly, despite evidence that nonnative species are less affected by local pathogens (Callaway et al., 2004), we found no difference in response between native and nonnative species. However, congeners did respond similarly to the *Fusarium* treatment, supporting previous work that found that more closely related species are more likely to share pathogens (Gilbert and Webb 2007; Parker et al., 2015). If applicable to a wider range of pathogens, our results suggest that changes in abiotic conditions, such as alterations in precipitation driven by global climate change, may influence plant community composition through changes in the effective specialization of pathogens.

The abiotic context-dependency in plant-pathogen interactions that we observed suggests that microbe-mediated shifts in plant community composition can occur without a change in microbial community composition. Studies that find changes in plant-microbe interactions under different abiotic conditions may investigate whether changes in microbial community composition relate to changes in plant responses. In some cases, there is evidence that shifts in microbial taxa may be involved (Lagueux et al., 2020), but in others, no taxa of putative importance were identified (Dudenhöffer et al., 2022). If microbial effects are context dependent, as we found, differences in microbial community taxa may not provide mechanistic insights into climate-mediated shifts in plant-microbe interactions. Importantly, this may hinder our ability to predict plant community change or manage microbial communities to avoid the consequences of climate change. A caveat to our results is that we did not track how the background microbial community (or the *Fusarium*) responded to our treatments. Changes in the composition of the background community could have modified the effect of the *Fusarium* on the plant species. Similar experiments that track the relative abundance of the inoculated pathogen and the background community could help resolve these potential interactions.

Contrary to our prediction that nonnative species would be less affected by the pathogen, native and nonnative species did not respond differently to the *Fusarium*. The Enemy Release Hypothesis predicts that nonnative species may gain a fitness benefit in their new ranges by escaping from pathogens (Callaway et al., 2004), and experiments and meta-analyses have found support for the Enemy Release Hypothesis (Mitchell and Power, 2003). The pathogen we used was cultured from a common grass in the coastal prairie, *Andropogon gerardii*, which was not used in the experiment. Therefore, it is possible that all the species were relatively novel hosts. While the origin of plant species was not a strong predictor of pathogen response, plant species from the same genus responded similarly to the pathogen. This is in line with previous work showing that plant relatedness may be a good predictor of plant-pathogen interactions (Crawford et al., 2019). In particular, more closely related plant species are more likely to share pathogens (Gilbert and Webb 2007; Parker et al., 2015).

The switch from low species specificity in dry conditions to higher species specificity in wetter conditions coincided with a shift from the *Fusarium* weakly benefiting the plants to strongly negatively affecting some plant species. While the majority of documented plant-microbe interactions involving *Fusarium* species are negative, there are some instances of *Fusarium* species benefiting plants. This includes *F. verticillioides,* which can protect corn from other fungal pathogens (Estrada et al., 2012). The mechanism by which this *Fusarium* isolate benefited

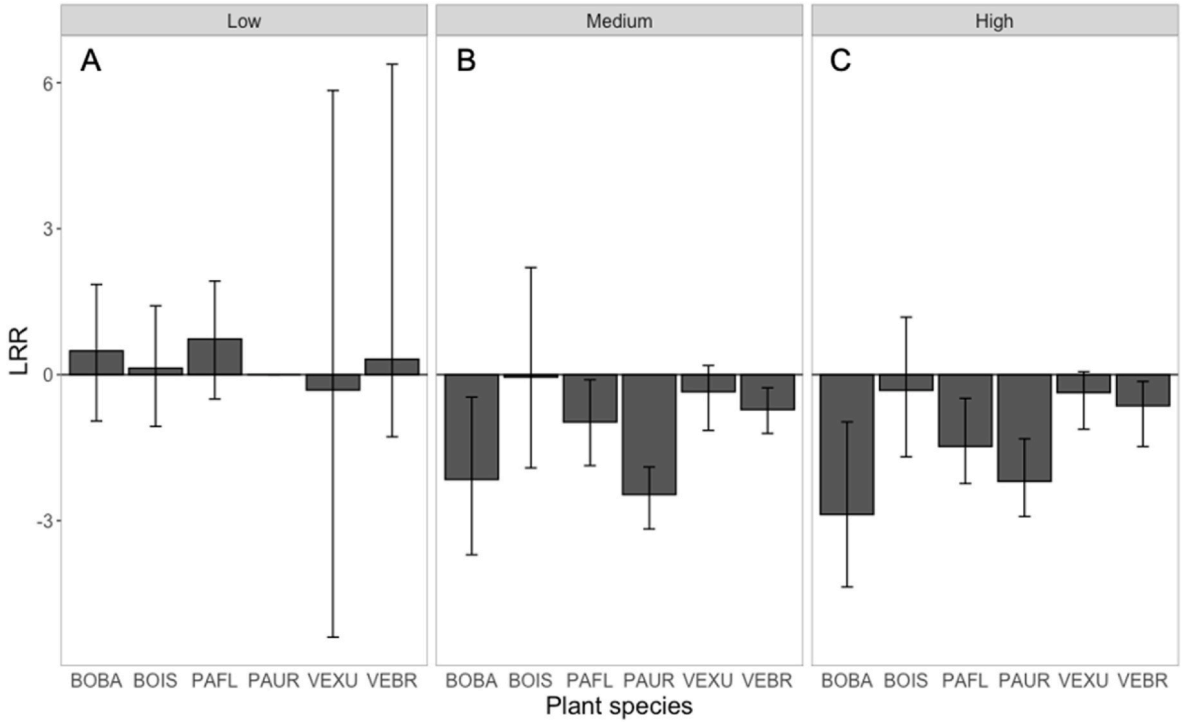

Fig. 2. The log response ratio (LRR) for the effect of *Fusarium* on total biomass of six plant species (BOBA = *Bothriochloa barbinodis*, BOIS = *Bothriochloa ischaemum*, PAFL = *Paspalum floridanum*, PAUR = *Paspalum urvillei*, VEXU = *Verbena xutha*, VEBR = *Verbena brasiliensis*) across three watering treatments [low (A), medium (B), high (C)]. Positive values indicate a positive effect of the *Fusarium* on plant biomass and negative values indicate a negative effect of *Fusarium* on plant biomass. Bars are bootstrapped averages with 95% confidence intervals. Bars that overlap zero indicate that the *Fusarium* did not differentially influence plant biomass.

Table 2
Results from a mixed effect model testing the effects of water treatment, *Fusarium* treatment, plant origin (native, nonnative), and all possible interactions on a total biomass. Bold *P*-values are statistically significant at $P < 0.05$.

	df	*F*	*P*
Water	2, 344	75.3813	**< 0.0001**
Fusarium	1, 344	35.2238	**< 0.0001**
Origin	1, 4	0.0027	0.9611
Water × *Fusarium*	2, 344	19.5991	**< 0.0001**
Water × origin	2, 344	0.0632	0.9388
***Fusarium* × origin**	1, 344	0.9965	0.3189
Water × *Fusarium* × origin	2, 344	0.7424	0.4768

plants in dry conditions is unknown. Recently, it was found that bacterial strains with traits that help the bacteria tolerate dry conditions also help plants tolerate dry conditions, possibly through byproduct benefits which occur when traits that benefit one species provide incidental benefits to another species with no direct cost to the provider (Bolin et al., 2022). If *Fusarium* is behaving similarly, byproduct benefits could help explain the low species specificity in the beneficial effects. Alternatively, the *Fusarium* isolate may be acting as a mutualist in low water conditions, helping plants uptake water in exchange for plant carbon – similar to arbuscular mycorrhizal fungi or dark septate fungi (Auge, 2001). If so, in wetter conditions the interaction may become parasitic as the plant no longer benefits from the fungus. However, this would not necessarily explain the switch in species specificity of the interactions.

Predicting how plant communities will respond to climate change is a challenge for community ecology, as the interactions that structure plant communities can be modified by climate. Specialist enemies, in particular, have been noted for their potential to play a key role in structuring plant communities (Janzen, 1970; Connell, 1983; Bever et al., 2015). However, the effective specialization of pathogens (i.e., the same pathogen having different effects on each of its host species) offers an avenue for generalist pathogens to contribute to plant species coexistence, for example through negative plant-soil feedback or Janzen-Connell effects (Benítez et al., 2013). Importantly, if pathogen effective specialization is dependent on the climate, then the mechanisms that structure plant communities may shift with the climate. A more thorough understanding of the context-dependency of plant-pathogen interactions, including developing predictions for when to expect effective specialization, may play an important role in predicting how plant communities will respond to climate change.

Author contributions

Jakob Joachin and Kerri M. Crawford conceptualized the study with input from Elliot Lagueux, and Noah C. Luecke. Jakob Joachin and Camryn Kritzell conducted the experiment and collected experimental data. Kerri M. Crawford analyzed the data with input from all authors. Jakob Joachin and Kerri M. Crawford led manuscript preparation. All authors edited the manuscript.

5. Data availability

Data are provided as a supplemental file for review and publication.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Kerri Crawford reports financial support was provided by National Science Foundation.

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floridanum, and Scott Clark for collecting seeds of *V. brasiliensis*. Collection of the fungal isolate was funded by NSF DEB#1456955 to Jennifer Rudgers. This work was funded by an NSF REPS supplement to NSF DEB Award # 1754287.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2023.101286.

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