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Intraspecific and biogeographical variation in foliar fungal communities and pathogen damage of native and invasive *Phragmites australis*

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Abstract

Aim: Recent research has highlighted that the relationship between species interactions and latitude can differ between native and invasive plant taxa, generating biogeographical heterogeneity in community resistance to plant invasions. In the first study with foliar pathogens, we tested whether co-occurring native and invasive lineages of common reed (*Phragmites australis*) exhibit non-parallel latitudinal gradients in foliar fungal communities, pathogen susceptibility and damage, and whether these biogeographical patterns can influence the success of invasion.

Location: North America.

Time period: 2015–2017.

Major taxa studied: Perennial grass *P. australis*.

Methods: We surveyed 35 *P. australis* field populations, spanning 17° latitude and comprising four phylogeographical lineages, including one endemic to North America and one invasive from Europe. For each population, we quantified the percentage of leaf pathogen damage and cultured fungi from diseased leaves, which we identified using molecular tools. To assess whether latitudinal gradients in pathogen damage had a genetic basis, we inoculated plants from 73 populations with four putative pathogens in a complementary common garden experiment and measured *P. australis* susceptibility (i.e., diseased leaf area).

Results: We isolated 84 foliar fungal taxa. *Phragmites australis* lineage influenced fungal community composition but not diversity. Despite the invasive European *P. australis* lineage being the least susceptible to three of the four pathogens tested in the common garden experiment, pathogen damage in the field was similar between native and invasive lineages, providing no evidence that release from foliar pathogens contributes to the success of invasion. Genetically based latitudinal gradients in pathogen susceptibility observed in the common garden were isolate specific and obscured by local environmental conditions in the field, where pathogen damage was threefold higher for northern compared with southern populations, regardless of lineage.

Main conclusions: Our results highlight that host plant lineage and genetically based biogeographical gradients strongly influence foliar fungal communities and pathogen susceptibility, but do not translate to patterns of pathogen damage observed in the field.

KEYWORDS

biotic resistance, diversity, endophytes, enemy release, genotype, invasive plant, latitudinal gradients, native plant, *Phragmites australis*, plant–fungi interactions

1 | INTRODUCTION

Biological invasions threaten biodiversity and ecosystem function at a global scale (Mack et al., 2000). The success of invasive plants is increasingly being recognized as strongly influenced by their associated fungi, acting through a variety of direct and indirect interactions involving plant antagonists (i.e., pathogens) and mutualists (i.e., endophytes and mycorrhiza) (Dickie et al., 2017). For example, invasive plants may be successful because they escape fungal pathogens (the enemy release hypothesis: Elton, 1958; Keane & Crawley, 2002; Mitchell & Power, 2003), engage in diverse and strong direct interactions with fungal mutualists (the enhanced mutualism hypothesis: Reinhart & Callaway, 2006) or interact indirectly with other plants through spillover, spillback and soil legacies (Allen, Meyerson, Flick, & Cronin, 2018; Mangla & Callaway, 2008; Power & Mitchell, 2004). Conversely, pathogens can also have strong negative impacts on invaders (biotic resistance: Elton, 1958; Flory, Alba, Clay, Holt, & Goss, 2018), whereas other studies have found no differences between native and invasive plants in their interactions with fungal pathogens and mutualists (Bunn, Ramsey, & Lekberg, 2015; van Kleunen & Fischer, 2009). Whether invasive plants gain a systematic advantage over native species through their interactions with fungi remains an open question.

Studies of invasion hypotheses invoking biotic interactions have generally focused on small spatial scales, ignoring the possibility that the strength of these interactions could vary over broader geographical scales. Biogeographical variation in how species interactions influence invasion success might exist because the diversity, specialization and strength of species interactions are all expected to increase closer to the equator (the latitudinal diversity gradient: Hillebrand, 2004; Kinlock et al., 2018; and the biotic interactions hypothesis: Coley & Kursar, 2014; Dobzhansky, 1950; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009). However, empirical evidence of latitudinal gradients in the specialization and strength of biotic interactions has been highly variable (Anstett, Nunes, Baskett, & Kotanen, 2016; Moles, Bonser, Poore, Wallis, & Foley, 2011; Moles & Ollerton, 2016; Ollerton, 2012), highlighting the need for an improved understanding of the mechanisms underlying these mixed results. For example, because of their different ecological and evolutionary histories, native and invasive taxa may be expected to experience non-parallel latitudinal gradients in specialization or species interaction strength, which could generate biogeographical heterogeneity in the strength of enemy release or biotic resistance. To date, this hypothesis has been tested with varying levels of support for a range of direct and indirect plant–herbivore interactions (Allen et al., 2017; Bhattarai, Meyerson, Anderson, et al., 2017; Bhattarai, Meyerson, & Cronin, 2017; Cronin, Bhattarai, Allen, & Meyerson, 2015; Lu et al., 2019) but has not been examined for plant–microbe interactions. The one exception is the recent study by Lu, He, Ding, and Siemann (2018), who found that native and invasive *Alternanthera* species in China differed in their response to soil-borne enemies from along a latitudinal gradient, influencing the performance of a shared flea beetle herbivore (*Agasicles hygrophila*) and resulting in stronger enemy release at lower latitudes.

For fungi, evidence for latitudinal diversity gradients has been mixed, with the direction and magnitude of relationships often depending on the functional group of the fungi. For example, pathogen, saprotroph and endophyte diversity appear to increase towards the equator (Tedersoo et al., 2014; Terhonen et al., 2011; Wellman, 1968; but see Millberg, Boberg, & Stenlid, 2015), whereas results for mycorrhiza and various combinations of functional groups are more inconclusive (Kinlock et al., 2018; Öpik et al., 2010; Tedersoo et al., 2014). However, results have often been confounded by changes in host plant species richness and identity, and phylogenetically controlled tests using a single host plant species over a broad latitudinal gradient are rare (Lu et al., 2018; Millberg et al., 2015; Terhonen et al., 2011). Fewer studies have examined latitudinal variation in fungal pathogen damage or plant susceptibility to pathogens, but both positive and negative gradients have been reported (Björkman, 1963; Burdon, Oates, & Marshall, 1983; Hamilton et al., 2013). Finally, for studies that are conducted in the field, local environmental conditions may alter the expression of genetically based latitudinal gradients in plant resistance or susceptibility to natural enemies. It is therefore important that field surveys of pathogen abundance, diversity or composition be paired with controlled greenhouse or common garden experiments (e.g., Bhattarai, Meyerson, Anderson, et al., 2017). To date, this combined approach has not been taken with pathogens of invasive species.

The widespread co-occurrence of multiple native and introduced phylogeographical lineages of *Phragmites australis* (Cav.) Trin. ex Steudel (common reed; hereafter, *Phragmites*) in North America presents an ideal system in which to examine how latitudinal variation in plant–fungal interactions can influence the success of invasion (Cronin et al., 2015; Meyerson, Cronin, & Pyšek, 2016). By

minimizing phylogenetic and environmental differences, the multiple *Phragmites* lineages allow for robust comparison of the interactions of foliar fungi with native and introduced plant taxa (*Phragmites*) along a biogeographical gradient (see also Lu et al., 2018). Using a field survey and complementary common garden experiment, we tested the following predictions (also summarized in Figure 1): (a) introduced *Phragmites* lineages have lower foliar fungal diversity and fewer fungal pathogens and suffer less pathogen damage than the native lineage (i.e., the enemy release hypothesis); (b) foliar fungal communities, pathogen damage and *Phragmites* susceptibility to pathogens vary along a latitudinal gradient; (c) native and invasive *Phragmites* lineages exhibit non-parallel latitudinal gradients in foliar pathogen damage and susceptibility; and (d) latitudinal gradients observed in the field are repeated in a common garden experiment (i.e., are genetically based).

2 | MATERIALS AND METHODS

2.1 | Study organisms

Phragmites australis is a tall perennial grass with a cosmopolitan distribution and is considered a model organism for studying plant invasions (Meyerson et al., 2016). Multiple phylogeographical lineages of *Phragmites* co-occur in North America (Lambertini et al., 2012; Meyerson, Lambertini, McCormick, & Whigham, 2012; Saltonstall, 2002). The native lineage in North America is endemic and widespread, but an invasive lineage of *Phragmites* from Europe (also known as haplotype M, but hereafter referred to as the European lineage) has spread rapidly in North America since first appearing in herbarium records 150 years ago (Meyerson et al., 2012; Saltonstall, 2002). This European lineage forms large, dense monocultures that provide ecosystem services such as protection from erosion and carbon storage, but also have negative impacts on hydrology, native biodiversity and ecosystem function (reviewed by Meyerson, Saltonstall, & Chambers, 2009). A closely related lineage known as Delta, originating from the Mediterranean (Lambertini et al., 2012), has been reported only from the Mississippi River Delta in Louisiana (Hauber, Saltonstall, White, & Hood, 2011; Knight et al., 2018). A fourth lineage, known as Gulf, is widely distributed along the Gulf of Mexico and west to California (Lambertini et al., 2012; Meyerson et al., 2012), is likely to be a recent arrival from Mexico or Central America (Colin & Eguiarte, 2016) and is spreading (Bhattarai & Cronin, 2014).

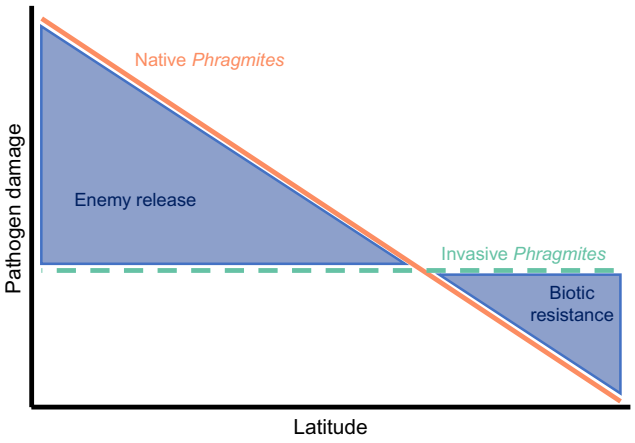

FIGURE 1 Predicted relationship between population latitude and pathogen damage for native (continuous line) and invasive (dashed line) lineages of *Phragmites australis* in a North American field survey and Louisiana common garden experiment. Adapted from Bezemer, Harvey, and Cronin (2014) and Cronin et al. (2015) [Colour figure can be viewed at wileyonlinelibrary.com]

The diversity and function of the *Phragmites* microbiome have been investigated (for review, see Kowalski et al., 2015). Distinct oomycete, archaean and bacterial communities have been reported from rhizosphere soil of native and European *Phragmites* lineages in North America (Bowen et al., 2017; Crocker, Karp, & Nelson, 2015; Nelson & Karp, 2013; Yarwood, Baldwin, Gonzalez Mateu, & Buyer, 2016), although no differences were detected for fungal, bacterial and oomycete root endophyte communities in the Great Lakes region (Bickford, Goldberg, Kowalski, & Zak, 2018). However, *Phragmites* foliar fungal communities (i.e., pathogens and non-symptomatic endophytes) and their impacts have yet to be compared formally among native and invasive lineages (but for a local-scale survey in New York, see Shearer & Harms, 2012). Almost nothing has been reported to date regarding the ecology of the Gulf or Delta lineages (but see Allen et al., 2018; Bowen et al., 2017). Thus, this study provides one of the first comparisons involving more than the two most common North American *Phragmites* lineages and is the first to examine differences in foliar fungal communities of *Phragmites* lineages in North America.

Finally, latitudinal gradients in plant nutritional condition, structural and chemical defenses, palatability to herbivores, herbivore damage, apparent competition strength and tolerance to leaf tissue damage have previously been described for *Phragmites* and often differ between the native and invasive lineages (Allen et al., 2017; Bhattarai, Meyerson, Anderson, et al., 2017; Bhattarai, Meyerson, & Cronin, 2017; Cronin et al., 2015). However, this is the first study to compare latitudinal gradients in foliar fungal community structure and plant–pathogen interactions between any native and invasive taxa.

2.2 | Field survey of pathogen damage and fungal communities

To examine interactions between *Phragmites* and foliar fungi, we surveyed 35 *Phragmites* populations (10 native, 10 European, 10 Gulf and five Delta) along the east coast of the USA from south Florida (26.6°) to Maine (44.0°) and along the Gulf Coast of Louisiana (Supporting Information Appendix S1). East Coast populations represent where the invasive Eurasian lineage first appeared in herbarium records *c*. 150 years ago. Populations of different lineages often occurred in the same watershed (same

population location in Supporting Information Appendix S1) but were rarely intermixed. Populations in Louisiana were included because of the co-occurrence of two additional non-native lineages of *Phragmites*, but were not considered for latitudinal analyses because of their limited geographical range that did not overlap with the native and European lineages. Leaf material from each population was collected for later determination of lineage (based on chloroplast DNA) using the methods of Saltonstall (2002) with modifications outlined by Kulmatiski, Beard, Meyerson, Gibson, and Mock (2010). The Delta lineage was identified based on morphology and flowering phenology (Hauber et al., 2011). Sampling was conducted in the late summer of 2015, from 28 July to 12 September, from south to north along the latitudinal gradient of native and European populations (all were flowering at the time of sampling), followed by the Gulf and Delta populations. Although populations were visited on only one occasion, *Phragmites* leaves persist throughout the growing season, meaning that our sampling design should estimate cumulative foliar pathogen damage and minimize phenological variation.

The proportion of stems with diseased leaves (i.e., presence of spots, lesions, discoloration or chlorosis) was estimated by walking transects from the edge to the interior of each population, examining the closest stem every metre for pathogen damage, until a total of 50 stems was reached. For 10 randomly selected stems that had pathogen damage, the number of leaves with and without pathogen damage were counted to determine the proportion of leaves damaged. Finally, the severity of damage by pathogenic fungi was quantified by photographing and estimating the percentage of area from 20 independent, randomly selected diseased leaves that had symptoms of pathogen damage per population using ImageJ software (Rasband, 2018). The overall percentage of leaf tissue area with symptoms of disease for each population was calculated as the proportion of stems with pathogen damage multiplied by the proportion of leaves per stem with pathogen damage multiplied by the percentage of leaf area with disease symptoms.

For culturing and identification of putative fungal pathogens and other endophytic fungi, we used the same 20 diseased leaves that were photographed to estimate pathogen damage. The leaves were stored in an ice chest, transported back to Louisiana State University, and processed the following day. Leaves were surface sterilized by sequential immersion and agitation in 95% ethanol, 5% sodium hypochlorite solution and 70% ethanol (U'Ren et al., 2014). Using a sterilized hole punch (2 min in 5% sodium hypochlorite solution), tissue samples 3 mm in diameter were taken from the margins of symptomatic tissue and plated on water agar (17 g agar and 1 L H_2O) for isolation of emergent fungi. Plates were stored in an environmental chamber (21°C, 50% relative humidity, 16–8 hr light–dark cycle) and checked every 2–3 days for fungal growth. Emergent fungi were isolated and grown as pure cultures on potato dextrose agar (PDA; 5 g agar, 7.6 g PDA and 1 L H_2O), with leaf tissue samples regularly yielding multiple fungal isolates. Each isolate was transferred to a corn meal agar (CMA; 6 g agar, 8.5 g CMA and 1 L H_2O) slant for long-term storage at 4°C.

The PDA cultures were photographed and identified to morphospecies based on colour, growth characteristics and spore morphology, following Lacap, Hyde, and Liew (2003). Confirmation of morphospecies was conducted using DNA barcodes, detailed in the Supporting Information (Appendix S2). Finally, to investigate differences in the prevalence of potential pathogens among lineages, we obtained putative function(s) (pathogen, saprophyte, endophyte or epiphyte) for each identified taxon based on the FUNGuild database (Nguyen, Song, et al., 2016; Supporting Information Appendix S3) and used these data to calculate relative pathogen abundance (i.e., the proportion of isolates per population that were identified as potential pathogens) for each *Phragmites* population.

2.3 | Common garden pathogen susceptibility experiment

A complementary common garden experiment was conducted in 2017 at Louisiana State University (30.36° N, 91.14° W) to assess whether the susceptibility of *Phragmites* to individual isolates of potential pathogens varied among lineages and with latitude of origin. The open-air common garden included 73 *Phragmites* populations (20 native, 27 European, 19 Gulf and seven Delta) from throughout North America, ranging in latitude from 26.1° to 47.4° (2,245 km; Supporting Information Appendix S4). Plants were grown from rhizome fragments in 75 L pots with a sand substrate and regularly fertilized with Osmocote® (9 month, slow-release 15–9–12 NPK, The Scotts Miracle-Gro Company®, Marysville, OH, USA) and Ironite® (Pennington®, Madison, GA, USA). Plants were grown in the common garden for ≥ 2 years before being potted for the experiment to control for source population maternal effects, and panicles were removed before reaching maturity to prevent sexual reproduction and crossing among populations. For every pot in the garden (some *Phragmites* populations were planted in more than one pot), we inoculated plants with four different potential pathogens obtained from our field survey (one stem per pathogen per pot), selected because they were isolated from all four lineages, associated with diseased leaf tissue and were identified as putative pathogens (Supporting Information Appendix S4). They were identified as *Stagonospora* sp. (isolated from the Gulf lineage in Florida), *Cladosporium* sp. (one isolate each from the Delta and Gulf lineages in Louisiana) and *Alternaria alternata* (from the native lineage in Maine).

To create spore solutions for inoculation, pure sporulated cultures of each isolate were flooded with 10 ml of 0.05% Tween-20 and mycelia scraped using a sterile metal spatula to release the spores. The resulting suspension was centrifuged for 5 min at 2,000 ×*g* and 25°C and then filtered through cheese cloth to remove mycelia. Spore concentration was quantified using a haemocytometer and adjusted to a final concentration of 1×10^5 spores/ml. A healthy *Phragmites* leaf, third or fourth from the top of the stem, was chosen for inoculation. Leaves were prepared by surface sterilization with 75% ethanol, before a small piece of sanding sponge was twice turned through 180° on the leaf adaxial surface *c*. 1.5 cm from the leaf base, to create an abraded area

of *c*. 0.5 cm^2. Inoculations were performed on 6 or 7 April 2017, using a method modified from Li et al. (2014). To perform each inoculation, 0.2 ml of spore solution (or deionized water for the control) was pipetted onto a cotton ball. The treated part of the cotton ball was placed on the abraded leaf surface and secured with tape. The cotton balls were wetted twice per day with deionized water and fungi allowed to grow for 6 days, when infected leaves were removed and photographed for determination of the total damaged area using ImageJ.

2.4 | Data analysis

Field survey data were subjected to a two-stage analysis. First, pathogen damage (percentage of leaf tissue area with disease symptoms) and foliar fungal diversity metrics (isolate abundance, rarefied richness, Shannon diversity and relative pathogen abundance) were compared among the four *Phragmites* lineages (native, European, Gulf and Delta) using ANOVA and Tukey's post hoc tests (Bonferroni corrected where appropriate). The richness of fungal taxa was rarefied to six isolates, the lowest number of fungi isolated from a population. Latitude was not included as a covariate in these models because populations of the Gulf and Delta lineages had very narrow latitudinal ranges relative to the native and European *Phragmites* lineages (3.7°).

The second stage of analyses involved testing for the presence of latitudinal gradients in pathogen damage and foliar fungal diversity for only the native and European *Phragmites* lineages. Owing to the number of potential explanatory variables arising from testing for both linear and nonlinear latitudinal gradients and their interactions with *Phragmites* lineage, we used the Akaike information criterion corrected for small sample size (AICc) to select the best-fitting mixed-effect models from a set of candidate models for each response variable (Burnham & Anderson, 2010). The full model included the explanatory variables of *Phragmites* lineage, a linear and nonlinear (latitude^2) term for latitude, and their interactions with lineage (total of five variables). Candidate models were based on subsets of the full model, using all possible combinations of the explanatory variables, but with the restriction that main effects must also be present in models containing interactions. We ranked candidate models from lowest to highest AICc and models with ΔAICc (= $AICc_i - AICc_{min}$) of two or less were deemed to have substantial support (Burnham & Anderson, 2010). When multiple supported models were identified, the best-fitting model was used for post hoc analyses, along with plausible models that contained any additional variables, meaning that each influential variable was subjected to post hoc tests (these are the results that we report below).

Differences in the community composition of foliar fungi were analysed using a similar two-stage approach. A principal coordinates analysis was performed on Bray–Curtis dissimilarities calculated from abundances of fungal taxa and community composition compared among *Phragmites* lineages and population latitude using PERMANOVA with 999 permutations. We drilled down into significant interaction terms using post hoc pairwise PERMANOVAs to compare lineages. To examine differences in beta diversity (i.e., similarity of populations within lineage) among lineages and satisfy PERMANOVA assumptions, we tested for multivariate homogeneity of dispersion. Like the richness and diversity metrics, we excluded the Gulf and Delta lineages from analyses of latitudinal gradients in community composition. We also calculated the pairwise geographical distance between all populations within each lineage and used linear regression to test whether populations closer to one another had more similar fungal communities. Singleton taxa do not provide information on community similarity and were removed before these analyses.

For each inoculated leaf in the common garden experiment, we computed the leaf area with pathogen damage, which was then ln-transformed to satisfy normality of residuals. We analysed each putative pathogen isolate separately, using the same two-stage data analysis approach as described above for the field survey. First, we used a linear mixed model with population included as a random effect (retained in all models) to test whether the damaged area differed among *Phragmites* lineages. Second, we used model selection to assess whether genetically based latitudinal gradients in susceptibility existed for any of the four pathogens. As before, we used a linear mixed model with *Phragmites* lineage, latitude and latitude^2 and their interactions considered in the full model, with population treated as a random effect. All analyses were conducted with R v.3.6.1 (R Development Core Team, 2019), using the packages vegan (Oksanen et al., 2019), lme4 (Bates et al., 2019), MuMIn (Bartoń, 2019) and emmeans (Lenth, Singmann, Love, Buerkner, & Herve, 2019). Analysis code is available upon request from the corresponding author.

3 | RESULTS

3.1 | Pathogen damage increased with latitude in the field

The percentage of leaf tissue area with disease symptoms was 3.3% ± 0.5% (mean ± SE) and ranged from 0.4% to 9.5% among populations. Pathogen damage did not differ among *Phragmites* lineages in the field ($F_{3,31}$ = 0.17, p = .916). Model selection identified two plausible models (ΔAICc ≤ 2) with equal support (AICc weight = .5) to explain variation in pathogen damage, containing latitude and latitude^2, respectively (Supporting Information Appendix S5). Foliar pathogen damage was almost four times higher at the northern than at southern end of our 993 km sampling distribution ($F_{1,18}$ = 5.74, p = .028, R^2 = .24), regardless of *Phragmites* lineage (Figure 2).

3.2 | Fungal communities differed among *Phragmites* lineages but did not change significantly with population latitude

A total of 717 fungal isolates were obtained from the field survey and used for analyses. These cultures were separated based on

molecular analyses or original morphospecies designation if molecular analyses were unsuccessful, resulting in 84 taxa (Supporting Information Appendix S3). The fungal taxa accumulation and rarefaction curves for the entire survey, each *Phragmites* lineage and individual populations (Supporting Information Appendix S6) indicated that we captured less than half of the total *Phragmites* endophyte and pathogen diversity in the sampled area (estimated as 182 ± 44 fungal taxa using the Chao1 diversity estimator). Of the fungal taxa that were sampled, only 7% were isolated from all four *Phragmites* lineages, whereas 67% were isolated from only a single lineage (Supporting Information Appendix S7).

The raw abundance of foliar fungal isolates differed among *Phragmites* lineages ($F_{3,31}$ = 3.67, p = .023) and was 51% higher from the native than the Delta lineage (p = .022; Table 1). Model selection identified a single plausible model (ΔAICc ≤ 2) containing only *Phragmites* lineage to explain the variation in isolate abundance per population (AICc weight = 1.00; Supporting Information Appendix S5), with Tukey's post hoc analyses finding 18% higher fungal isolate abundance from the native compared with the European lineage (p = .024). In contrast, rarefied richness did not differ among *Phragmites* lineages ($F_{3,31}$ = 1.14, p = .347; Table 1), and model selection deemed none of our explanatory variables to be influential (Supporting Information Appendix S5). Shannon diversity also did not differ significantly among *Phragmites* lineages ($F_{3,31}$ = 2.58, p = .071; Table 1). However, two plausible models were identified to explain variation in Shannon diversity, with the best-fitting model containing only the intercept (AICc weight = .73; Supporting Information Appendix S5) and the second model containing the main effects of latitude and latitude^2 (AICc weight = .27). Post hoc analyses revealed that the linear trend between latitude and Shannon diversity was not significant ($F_{1,17}$ = 0.40, p = .534), and the hump-shaped relationship was only marginally significant ($F_{1,17}$ = 3.37, p = .084). Finally, the relative abundance of pathogens also differed among lineages ($F_{3,31}$ = 6.04, p = .002) and was 2.3 and 2.8 times higher for the native than the Gulf (p = .008) and Delta (p = .014) lineages, respectively (Table 1). Model selection identified two plausible models (ΔAICc ≤ 2) to explain variation in pathogen relative abundance, containing the intercept only (i.e., no explanatory variables were considered to be influential; AICc weight = .63; Supporting Information Appendix S5) and *Phragmites* lineage (AICc weight = .37), respectively, with post hoc analyses revealing no significant difference between the native and European lineages (p = .221).

Foliar fungal community composition varied strongly among *Phragmites* lineages ($F_{3,31}$ = 6.87, p < .001; Figure 3), and subsequent pairwise PERMANOVA of Bray–Curtis dissimilarities revealed that all lineages differed from one another (all comparisons p < .003). Homogeneity of dispersion analysis revealed that all lineages had similar beta diversity ($F_{3,31}$ = 2.03, p = .131). Latitudinal gradients in community composition of foliar fungi depended on *Phragmites* lineage (latitude × lineage interaction; $F_{1,16}$ = 2.20, p = .029), with the similarity of populations increasing at higher latitudes for the native lineage ($F_{1,8}$ = 2.21, p = .046) but not for the European lineage

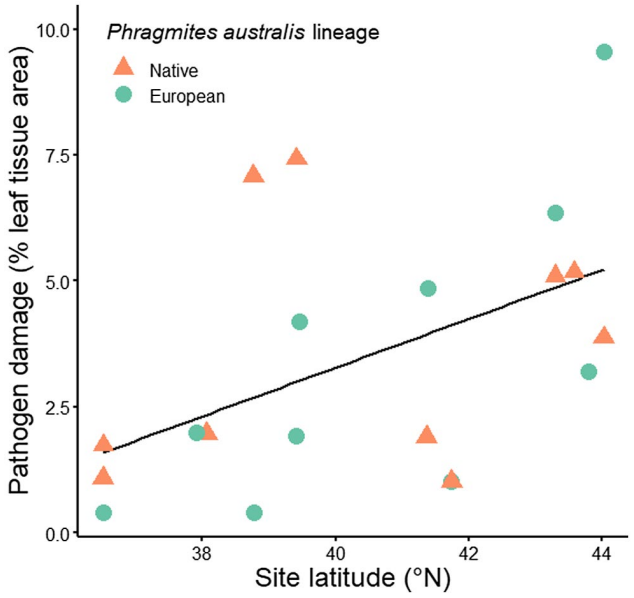

FIGURE 2 Relationship between population latitude and pathogen damage (percentage leaf tissue area with disease symptoms) for native (triangles) and European (circles) *Phragmites australis* lineages in the field survey. The line was fitted by least-squares regression for both lineages combined [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Average foliar fungal richness and diversity metrics per population (± SE) for diseased leaves from each *Phragmites australis* lineage examined in the field survey

	Phragmites australis lineage			
Parameter	**Native**	**European**	**Gulf**	**Delta**
Fungal isolate abundance	22.9 ± 1.09^{a}	19.4 ± 0.91^{ab}	22.0 ± 1.48^{ab}	15.2 ± 3.72^{b}
Total number of taxa	35	35	46	19
Singletons	11	8	13	4
Rarefied richness	4.1 ± 0.13^{a}	4.2 ± 0.20^{a}	4.5 ± 0.15^{a}	3.9 ± 0.42^{a}
Shannon diversity	1.8 ± 0.06^{a}	1.9 ± 0.12^{a}	2.0 ± 0.08^{a}	1.5 ± 0.21^{a}
Pathogen relative abundance	0.69 ± 0.04^{a}	0.58 ± 0.07^{ab}	0.30 ± 0.11^{b}	0.25 ± 0.09^{b}

Note: Different lowercase letters indicate significant differences between lineages for each diversity metric in Tukey's post hoc tests (p ≤ .05).

($F_{1,8}$ = 1.13, p = .344). These biogeographical patterns were also reflected in our findings that community dissimilarity increased with distance between populations for the native ($F_{1,88}$ = 4.44, p = .038) and Gulf ($F_{1,88}$ = 63.27, p < .001) lineages, was marginally significant for the European lineage ($F_{1,88}$ = 3.13, p = .080) and had no relationship for the Delta lineage ($F_{1,18}$ = 1.73, p = .205).

3.3 | Pathogen susceptibility varied with lineage latitude

In the common garden, we detected differences in pathogen damage (infection area) among *Phragmites* lineages for three of the four pathogens investigated: *Alternaria alternata* from Maine ($F_{3,68}$ = 4.86, p = .004) and *Cladosporium* sp. 1 ($F_{3,75}$ = 4.40, p = .007) and *Cladosporium* sp. 2 ($F_{3,79}$ = 3.52, p = .019), both from Louisiana. The European lineage suffered 36% (p = .007) and 52% (p = .005) less damage than the Gulf lineage against *Alternaria alternata* and *Cladosporium* sp. 1, respectively, and 34% (p = .030) less damage than the native lineage against *Cladosporium* sp. 2 (Figure 4). No other differences among lineages were detected.

Model selection identified four plausible models (ΔAICc ≤ 2) to explain variation in pathogen damage from *Alternaria alternata* (Supporting Information Appendix S8). The full model was the best fitting, containing the lineage × latitude and lineage × latitude^2 interactions, along with the associated main effects (AICc weight = .32). Pathogen damage to the European lineage demonstrated positive and U-shaped relationships with latitude ($t_{40.6}$ = −1.89, p = .067) and latitude^2 ($t_{40.8}$ = 1.92, p = .062), respectively, although these relationships were not significant at the α = .05 level. Conversely, pathogen damage of the native lineage significantly decreased with latitude ($t_{38.5}$ = 2.04, p = .049) and latitude^2 ($t_{38.4}$ = −2.17, p = .037; Figure 5a).

For both putative pathogens *Cladosporium* sp. 1 and *Cladosporium* sp. 2, model selection identified the top plausible model as containing only the *Phragmites* lineage main effect (AICc weights = .37 and 1.00, respectively; Supporting Information Appendix S8). For *Cladosporium* sp. 1, there was a non-significant trend towards lower damage on the European than the native *Phragmites* lineage ($F_{1,47}$ = 3.11, p = .084), whereas for *Cladosporium* sp. 2, there was significantly lower damage on the native compared with the European lineage ($F_{1,49}$ = 6.17, p = .016). For *Cladosporium* sp. 1, additional plausible models included main effects of latitude and latitude^2 (Supporting Information Appendix S8), although post hoc analyses found that their negative relationships with damaged area had only marginal significance at the α = .05 level ($F_{1,46}$ = 3.43, p = .071 and $F_{1,46}$ = 3.46, p = .069, respectively).

Finally, model selection identified five plausible models to explain variation in pathogen damage from *Stagonospora* sp. (Supporting Information Appendix S8). The two top models comprised the lineage × latitude (AICc weight = .31) and lineage × latitude^2 (AICc weight = .26) interactions and main effects. The European lineage showed a positive relationship with latitude (t_{74} = 2.81, p = .006) and latitude^2 ($t_{25.1}$ = 2.75, p = .011), whereas pathogen damage of the native lineage declined with latitude (t_{74} = −2.46, p = .016) and latitude^2 ($t_{25.2}$ = −2.42, p = .029; Figure 5b).

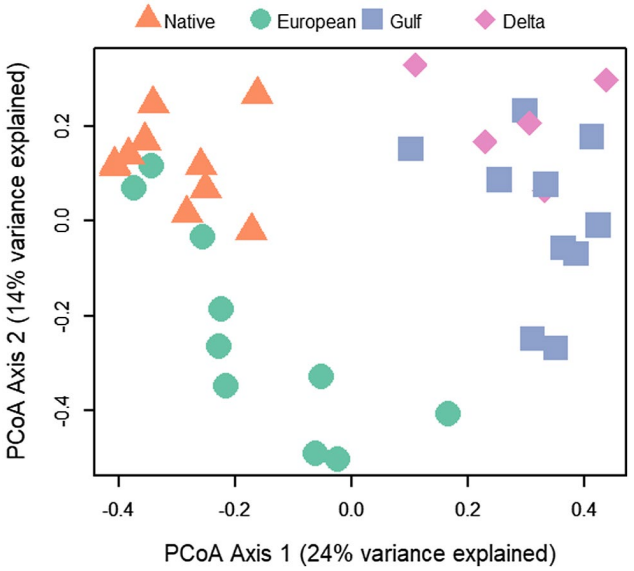

FIGURE 3 Ordination plot of principal coordinates analysis (PCoA) of Bray–Curtis dissimilarities among the fungal communities of diseased leaves from *Phragmites australis* populations belonging to four different lineages (native, European, Gulf and Delta). Each point represents a single *Phragmites* population, with points closer in ordination space having more similar fungal communities [Colour figure can be viewed at wileyonlinelibrary.com]

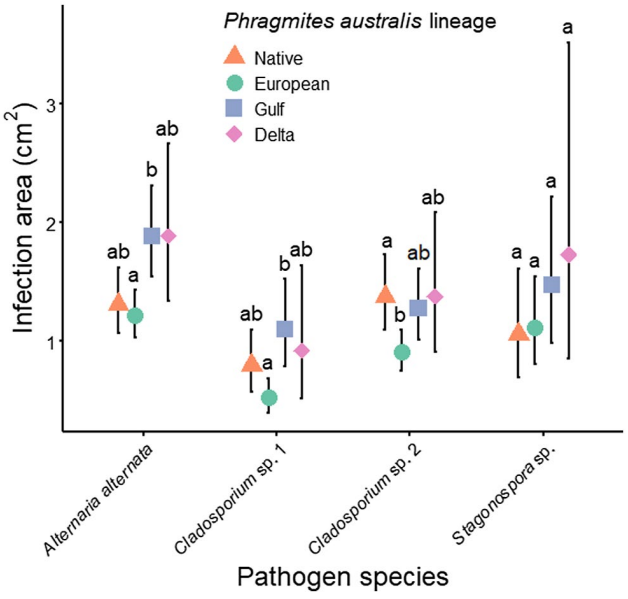

FIGURE 4 Area of infection (in square centimetres; back-transformed least-squares means ± 95% confidence intervals) of native, European, Gulf and Delta lineages of *Phragmites australis*, inoculated using spore solution from four foliar fungal isolates in a common garden experiment. Different letters indicate significant differences between lineages for each pathogen in Tukey's post hoc tests (p ≤ .05) [Colour figure can be viewed at wileyonlinelibrary.com]

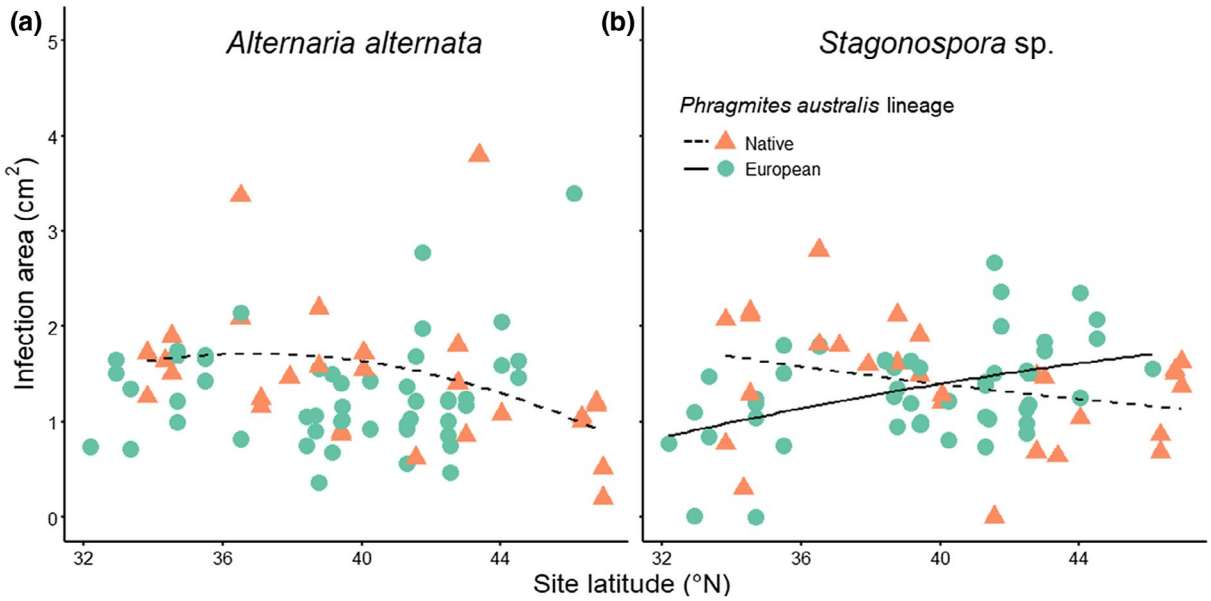

FIGURE 5 Relationships between population latitude and area of infection (in square centimetres) for populations of native and European *Phragmites australis* lineages inoculated with spore solutions from isolates of *Alternaria alternata* (a) and *Stagonospora* sp. (b) in a common garden experiment. Only lines (fitted by least-squares regression) significant at the α = .05 level are shown, meaning that there is no regression line presented for the European lineage in panel (a) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Recent studies have demonstrated the presence of biogeographical heterogeneity in enemy release resulting from non-parallel latitudinal gradients in the strength of plant–herbivore interactions (Allen et al., 2017; Bhattarai, Meyerson, Anderson, et al., 2017; Bhattarai, Meyerson, & Cronin, 2017; Cronin et al., 2015; Lu et al., 2018, 2019). In the first study to examine this possibility for plant–pathogen interactions, we found a positive latitudinal gradient in pathogen damage to *Phragmites* in the field, but despite possessing different fungal communities, the native and European lineages of *Phragmites* exhibited parallel gradients. This finding indicates that there is little biogeographical heterogeneity in enemy release from pathogens for European *Phragmites* along the Atlantic Coast of the USA. Conversely, in a controlled common garden environment, we found a mixture of parallel and non-parallel genetically based latitudinal gradients in pathogen susceptibility, depending upon the pathogen isolate being investigated. These mixed results demonstrate that biogeographical patterns in escape from enemies depend on the type of interaction (i.e., herbivores vs. pathogens) and focal species, suggesting that a more comprehensive assessment of species interactions might improve future studies that investigate latitudinal gradients in enemy release and biotic resistance. Furthermore, the differing results between the field and common garden indicate that the local environment can obscure genetically based patterns in plant traits associated with enemy interactions, such as susceptibility to pathogens (see also Allen et al., 2017; Bhattarai, Meyerson, Anderson, et al., 2017). This study is the first to examine empirically the contribution of genetics and local environmental conditions to latitudinal gradients in plant–pathogen interactions.

We found a high diversity of fungi associated with diseased *Phragmites* leaves; 717 fungal isolates comprising 84 fungal taxa. In contrast to our first prediction, fungal abundance, richness and diversity did not differ among *Phragmites* lineages. However, foliar fungal communities diverged among all four *Phragmites* lineages, overriding local environmental conditions associated with latitude. In other words, *Phragmites* populations of the same lineage (native or European) located at opposite ends of their distribution (i.e., North Carolina and Maine) generally had more similar fungal communities than plants of different lineages growing together in the same wetland, mirroring results for *Phragmites* rhizosphere bacteria (Bowen et al., 2017). Fungal communities also differed between the Gulf and Delta *Phragmites* lineages. However, their latitudinal ranges are very narrow (0.2° and 3.7°, respectively) and do not overlap with the distribution of the native and European lineages, potentially confounding biogeographical comparisons involving these two lineage groups. Our study adds to a growing body of evidence supporting plant lineage as a key determinant of foliar fungal community structure in multiple plant species (Materatski et al., 2019; Sapkota, Knorr, Jørgensen, O'Hanlon, & Nicolaisen, 2015; Whitham et al., 2012; but see Busby, Newcombe, Dirzo, & Whitham, 2014; Whitaker, Reynolds, & Clay, 2018). We expand on these earlier findings as one of the first studies conducted outside an agricultural context, by comparing closely related native and invasive taxa over a broad geographical scale and quantifying damage from the fungal pathogen community. For *Phragmites*, the divergent fungal communities for all lineage comparisons indicate a high degree of specialization of plant–fungal interactions at the lineage level, consistent with previous findings comparing rhizosphere oomycete (Crocker et al., 2015; Nelson & Karp, 2013), bacterial (Bowen et al., 2017) and archaean

(Yarwood et al., 2016) communities among *Phragmites* lineages, but contrasting with a recent study of endophytic root fungal, bacterial and oomycete communities in the Great Lakes region (Bickford et al., 2018). However, our study is the first to examine differences among *Phragmites* lineages in their foliar microbiome, where leaf tissue provides a substrate different from that of roots or the rhizosphere, which varies among *Phragmites* lineages in leaf chemistry (Cronin et al., 2015; Pyšek et al., 2019).

Our results from the field survey and common garden experiment present contrasting evidence for our first prediction and the enemy release hypothesis. Despite divergent foliar fungal communities and pathogen abundance, pathogen damage did not differ among *Phragmites* lineages in the field, suggesting that release from fungal pathogens does not contribute to the success of invasion by the European lineage (Bickford et al., 2018). However, the common garden experiment identified genetically based differences in susceptibility to some putative pathogens that favoured the European lineage over the Gulf and native lineages. This mismatch between field and common garden results might be because pathogen damage in the field is a cumulative measure of all pathogen damage, likely to be highly dependent upon local environmental conditions (e.g., edaphic and climatic factors, and the plant and pathogen community), whereas the common garden experiment assessed plant susceptibility to spore solutions from single isolates. Regardless, the combination of divergent fungal communities and genetically based differences in pathogen susceptibility among lineages raises the potential for the development of beneficial or pathogenic fungi to promote or control the native and European lineages, respectively. For example, fungal pathogens have previously been used for biological control (Evans, 2013; Harding & Raizada, 2015), although never at the subspecific level. Our study indicates that plant-associated fungi might represent a more diverse and tractable system for biological control ventures than insect herbivores, which, to date, have not proved sufficiently specialized for subspecific biological control (Bhattarai, Allen, Cronin, Kiviat, & Meyerson, 2016; Cronin, Kiviat, Meyerson, Bhattarai, & Allen, 2016; Kiviat et al., 2019). However, future research should focus on individual pathogen taxa and the link between pathogen damage and plant fitness.

Based on large-scale studies that have found higher plant pathogen and endophyte diversity at lower latitudes (Tedersoo et al., 2014; Terhonen et al., 2011; Wellman, 1968; but see Millberg et al., 2015), our second prediction was that *Phragmites* foliar fungal communities would vary along a latitudinal gradient. Contrary to this prediction, we found little evidence for latitudinal gradients in the abundance, richness and diversity of foliar fungi. These opposing results might be because many large-scale studies do not account for the confounding effect of concomitant gradients in host diversity, whereas we controlled for this effect by focusing on a single species. However, we observed latitudinal variation in fungal community structure for the native but not the European *Phragmites* lineage, indicating that the native lineage might be locally co-adapted with its fungal communities along the latitudinal gradient, whereas the European lineage might be interacting predominantly with widespread, generalist fungi, such as *Arthrinium* sp., isolated from six of the 10 European populations. Populations of the native lineage have a longer co-evolutionary history with resident fungal communities in North America than with the invasive lineages (millennia vs. *c*. 150 years; Orson, 1999), potentially leading to these more specialized interactions or altered plant resistance or tolerance to natural enemies. Interestingly, Lu et al. (2018) found a similar result for invasive *Alternanthera philoxeroides* (alligatorweed) and its native congener *Alternanthera sessilis* (sessile joyweed) in China, where the native *Alternanthera sessilis* exhibited latitudinal gradients in the composition and impact of rhizosphere soil bacteria and fungal communities, whereas no latitudinal gradients were observed for the invasive species. Taken together, these findings indicate that co-evolutionary history might play a substantial role in determining the composition and impact of the plant microbiome over large spatial scales.

Pathogen damage observed in the field survey was positively related to latitude, demonstrating biogeographical heterogeneity in plant–pathogen interactions. However, because the native and European *Phragmites* lineages exhibited parallel latitudinal gradients in pathogen damage, we find no evidence to support biogeographical heterogeneity in enemy release from pathogens for European *Phragmites* in North America. Our findings are consistent with the limited evidence for stronger pathogen pressure at higher latitudes (Nguyen, Castagneyrol, et al., 2016), but contrast with the absence of latitudinal gradients in fungal pathogen diversity on *Phragmites*, indicating that the positive latitudinal gradients in pathogen damage might be driven by other factors, such as increased pathogen virulence (Oates, Burdon, & Brouwer, 1983) or decreased plant resistance to pathogens (Burdon et al., 1983; but see Björkman, 1963; Hamilton et al., 2013) at higher latitudes. More broadly, our results contribute to the growing body of evidence supporting that several biotic interactions are not consistently stronger in the tropics, including meta-analyses of terrestrial herbivory (Moles et al., 2011), marine herbivory (Poore et al., 2012), seed predation (Moles & Westoby, 2003) and parasitism (Hawkins, 1994). To date, studies of plant–pathogen interactions have been scarce (Schemske et al., 2009). In contrast, both field experiments (Freestone, Ruiz, & Torchin, 2013) and meta-analysis (Kimbro, Cheng, & Grosholz, 2013) have presented evidence of stronger biotic resistance to invasive species at lower latitudes. However, a recent study showed that other influential mechanisms of invasion (i.e., propagule pressure) can overwhelm latitudinal variation in the impacts of predators on the population growth of bryozoans and tunicates (Cheng, Ruiz, Altieri, & Torchin, 2019), supporting other meta-analyses that revealed that biotic resistance of bird and freshwater communities did not vary with latitude (Alofs & Jackson, 2014; Blackburn & Duncan, 2001).

By simultaneously considering closely related native and invasive taxa, our study expands on these findings by demonstrating that native and invasive *Phragmites* experience identical latitudinal gradients in biotic resistance from foliar pathogens in the field. This lack of latitudinal variation in relative pathogen impact between native and invasive taxa does not favour the invader throughout its

range and suggests that this type of comparative approach is important when investigating biotic resistance as a potential mechanism of invasion success. Regardless, it remains an interesting question whether mechanisms of invasion success change frequently across the invaded range, such as has been proposed with *Spartina alterniflora* (smooth cordgrass) in China (Liu, Strong, Pennings, & Zhang, 2017). Interestingly, a recent analysis found ubiquitous support for biotic resistance using data on native and non-native species richness from 24,456 plots from 153 sites across the USA (Beaury, Finn, Corbin, Barr, & Bradley, 2020), but did not address whether its strength varied with latitude. Our findings of opposing latitudinal gradients in pathogen diversity (no gradient) and damage (positive gradient in the field, variable in the common garden) do not support natural enemy diversity as a driver of biotic resistance at the species level or the widely accepted notion that latitudinal gradients in diversity and interaction strength are related (Schemske et al., 2009).

We found mixed evidence for latitudinal gradients in plant–pathogen interactions in the common garden experiment, where genetically based latitudinal gradients in pathogen susceptibility differed between the native and European lineages (supporting our third prediction) and from those observed in the field (contrary to our fourth prediction). Native and European *Phragmites* lineages exhibited non-parallel latitudinal gradients in susceptibility to damage from two of the four isolates investigated in the common garden experiment (*Alternaria alternata* and *Stagonospora* sp.), indicating that the European *Phragmites* lineage might benefit from pathogen enemy release at lower latitudes, such as has been observed with some *Phragmites* herbivores (Cronin et al., 2015) and in the *Alternanthera* study system (Lu et al., 2018, 2019). However, these patterns in susceptibility did not translate to pathogen damage in the field, indicating that the local environmental conditions and plant and pathogen communities might be stronger determinants of pathogen damage than plant lineage alone. This conclusion is supported by several studies that demonstrate strong variation in pathogen damage and resistance along environmental gradients, including temperature, rainfall, humidity and elevation (Busby et al., 2014; Kniskern & Rausher, 2006; Spear, Coley, & Kursar, 2015), all of which may be expected to covary with latitude in the field. However, because the experiment was conducted in only one common garden, we cannot assess how changing environmental conditions in multiple common gardens could alter the latitudinal gradients in *Phragmites* pathogen susceptibility. Finally, the presence of a latitudinal gradient in susceptibility of the European lineage to *Stagonospora* sp. supports other research that has showed that invasive plants can evolve rapidly along latitudinal gradients (Bhattarai, Meyerson, Anderson, et al., 2017; Liu et al., 2020).

4.1 | Conclusions and future directions

This is the first study to compare foliar fungal communities, pathogen damage and genetically based pathogen susceptibility of native and invasive plant taxa along a latitudinal gradient. First, we show that the host plant lineage has a strong influence on foliar fungal community structure and pathogen susceptibility, but that this does not necessarily translate to differences in fungal diversity or pathogen damage in the field. Second, our results do not support the presence of latitudinal gradients in fungal abundance, richness or diversity. However, we show that pathogen damage of *P. australis* was positively related to latitude in North America and that native and invasive plant taxa can evolve non-parallel latitudinal gradients in foliar fungal community structure and pathogen susceptibility, with the latter varying among pathogen isolates. Finally, these pathogen-specific, genetically based latitudinal gradients in pathogen susceptibility might be dominated in the field by the influence of the local environmental conditions and pathogen community, resulting in no detectable biogeographical heterogeneity in enemy release for the European *Phragmites* lineage.

As with plant–herbivore interactions (Anstett et al., 2016), the jury remains out on the existence and direction of latitudinal gradients in plant–fungal interactions and the potential implications for fungal diversity. This uncertainty is largely attributable to the influence of many confounding factors and the methodological difficulties associated with assessing species interactions over such a large scale (Anstett et al., 2016; Moles et al., 2011). Therefore, because of the high variation in latitudinal gradients of species interactions, future research might aim to take a comprehensive, community-level and standardized approach to the assessment of latitudinal gradients in enemy release and biotic resistance and the role of species interactions in biological invasions in general. For example, this could be achieved by large-scale collaborative field surveys and exclusion experiments that quantify the impact on plant fitness of entire suites of important interaction partners (e.g., foliar fungi, mycorrhiza and herbivores) and also evaluate abiotic drivers of global change, such as salinity, nutrient availability and climate variables.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data have been archived in Dryad (https://doi.org/10.5061/dryad.n2z34tmsv), and all sequences were deposited into GenBank (NCBI) under accession numbers MT000583–MY000643.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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