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Intraspecific variation in indirect plant–soil feedbacks influences a wetland plant invasion

Warwick J. Allen,[1,2,4] Laura A. Meyerson,[3] Andrew J. Flick,[1] and James T. Cronin[1]

[1]*Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA*
[2]*The Bio-Protection Research Centre, Lincoln University, PO Box 84, Lincoln 7647 New Zealand*
[3]*Natural Resources Science, University of Rhode Island, Kingston, Rhode Island 02881 United States*

Abstract. Plant–soil feedbacks (PSFs) influence plant competition via direct interactions with pathogens and mutualists or indirectly via apparent competition/mutualisms (i.e., spillover to co-occurring plants) and soil legacy effects. It is currently unknown how intraspecific variation in PSFs interacts with the environment (e.g., nutrient availability) to influence competition between native and invasive plants. We conducted a fully crossed multi-factor greenhouse experiment to determine the effects of *Phragmites australis* rhizosphere soil biota, interspecific competition, and nutrient availability on biomass of replicate populations from one native and two invasive lineages of common reed (*P. australis*) and a single lineage of native smooth cordgrass (*Spartina alterniflora*). Harmful soil biota consistently dominated PSFs involving all three *P. australis* lineages, reducing biomass by 10%. Indirect PSFs (i.e., soil biota spillover) from the two invasive *P. australis* lineages reduced *S. alterniflora* biomass by 7%, whereas PSFs from the native *P. australis* lineage increased *S. alterniflora* biomass by 6%. Interestingly, interspecific competition and PSFs interacted to weaken their respective impacts on *S. alterniflora*, whereas they exerted synergistic negative effects on *P. australis*. *Phragmites australis* soil biota decreased *S. alterniflora* biomass when grown alone (i.e., a soil legacy), but increased *S. alterniflora* biomass when grown with *P. australis*, suggesting that *P. australis* recruits harmful generalist soil biota or facilitates *S. alterniflora* via spillover (i.e., apparent mutualism). Soil biota also reduced interspecific competition impacts on *S. alterniflora*, although it remained competitively inferior to *P. australis* across all treatments. Competitive interactions and responses to nutrients did not differ among *P. australis* lineages, indicating that interspecific competition and nutrient deposition may not be key drivers of *P. australis* invasion in North America. Although soil biota, interspecific competition, and nutrient availability appear to have no direct impact on the success of invasive *P. australis* lineages in North America, intraspecific lineage variation in indirect spillover and soil legacies from *P. australis* occur and may have important implications for co-occurring native species and restoration of invaded habitats. Our study integrates multiple factors linked to plant invasions, highlighting that indirect interactions are likely commonplace in influencing plant community dynamics and invasion success and impacts.

Key words: indirect interactions; interspecific competition; invasive species; nutrients; Phragmites australis; *soil biota; soil legacy;* Spartina alterniflora; *spillover.*

Introduction

Plant species influence the community composition and function of soil biota, which in turn can impact fitness of host plant species, a reciprocal interaction commonly referred to as a plant–soil feedback (PSF; Kulmatiski et al. 2008). The net impact of PSFs on host plants depends on the balance between beneficial (nitrogen-fixing bacteria, mycorrhizal fungi, and other mutualists) and harmful (soil-borne pathogens, parasites, and herbivores) interactions with soil biota (Klironomos 2002, Reinhart and Callaway 2006). PSFs have clear implications for the success of invasive plant species (van der Putten et al. 2013). For example, invasive plants could experience less positive (i.e., weaker associations with mutualists) or more negative (i.e., greater attack by local natural enemies) PSFs relative to closely related native species, suggesting some biotic resistance of the native soil community (Elton 1958, Callaway et al. 2013, Gribben et al. 2017). Alternatively, invasive plants may generate more positive or less negative PSFs than closely related native species, potentially resulting in dominance for the invader through the relative escape from natural enemies (i.e., the enemy release hypothesis; Elton 1958, Keane and Crawley 2002). Several empirical studies, meta-analyses, and reviews support this latter scenario (Klironomos 2002, Agrawal et al. 2005, Kulmatiski et al. 2008, Suding et al. 2013). Importantly, generalist soil biota cultivated by invaders also interact with co-occurring native plant species, resulting in indirect effects of the invasive species mediated through PSFs; i.e., pathogen/mutualist spillover, more generally known as apparent competition/mutualism (Eppinga et al. 2006, Mangla et al. 2008). Moreover, other plant species may also be inhibited by soil biota even after removal of the invasive plant; i.e., a soil legacy (Corbin and D'Antonio 2012, Grove et al. 2015).

Little is known about how PSFs interact with other factors linked to plant invasions such as competitive interactions with native species and nutrient availability. Modeling and experimental studies have demonstrated that even low

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[4] E-mail: warwick.j.allen@gmail.com

strength PSFs can alter interspecific competition (Bever 2003, Casper and Castelli 2007, Hodge and Fitter 2013), itself a key mechanism thought to underlie the success of invasive species (reviewed by Gioria and Osborne 2014). Likewise, anthropogenic nutrient deposition is a major component of global environmental change and a facilitating factor in many plant invasions (Dukes and Mooney 1999). Nutrient availability can alter competitive interactions (Wilson and Tilman 1993) and the activity of soil mutualists and pathogens, thus altering the direction and magnitude of PSFs (Manning et al. 2008). However, such a multi-factor approach has rarely been used to study the role of PSFs in invasion success (but see Larios and Suding 2015), despite having numerous interesting potential outcomes (summarized in Table 1).

Finally, intraspecific genetic variation is an important part of ecological and evolutionary processes (see Bolnick et al. 2011 for a review). It is known to alter the effects of nutrients (Saltonstall and Stevenson 2007) and competitors (Howard et al. 2008, Gomola et al. 2017) on plant fitness, and to influence community composition of soil biota (Schweitzer et al. 2008, Nelson and Karp 2013, Lamit et al. 2016, Bowen et al. 2017), yet experiments examining intraspecific variation in PSFs remain rare (but see Bukowski and Petermann 2014, Maron et al. 2015, Wagg et al. 2015, Bukowski et al. 2018). Biological invasions are often characterized by multiple introduction events, meaning multiple genetic lineages may be present in the introduced range (Durka et al. 2005, Meyerson et al. 2012, Gomola et al. 2017). Cryptic invasions have also been described (Saltonstall 2002, Tyler et al. 2007), where invasive genotypes or hybrids co-occur with native genotypes. Because many studies of invasive species assume that no intraspecific variation exists in their interactions with the environment and resident community, this can result in misleading insights and management recommendations, particularly if different genotypes employ different mechanisms of invasion (Meyerson and Cronin 2013, Gomola et al. 2017).

The goal of this study was to investigate the effects of plant intraspecific genetic variation, soil biota, and nutrient availability on competitive interactions between common reed, *Phragmites australis* (Cav.) Trin. ex Steudel, and a co-occurring native marsh grass species, smooth cordgrass (*Spartina alterniflora* Loisel.). In North America, there is a widespread endemic native lineage of *P. australis* as well as two invasive lineages (European and Gulf; Saltonstall 2002, Meyerson et al. 2009, 2012, Lambertini et al. 2012). We grew nine *P. australis* populations (three of each lineage) and a single population of *S. alterniflora* in pots containing live or sterilized soil inoculum from the rhizosphere of the respective *P. australis* population, at two nutrient levels, and with the plant species either alone or together. Based on invasion biology theory (i.e., the enemy release hypothesis) and the predominant pattern of invasive plants experiencing more positive PSFs than comparative native species (Klironomos 2002, Agrawal et al. 2005, Kulmatiski et al. 2008, Suding et al. 2013), we tested the following predictions: (1) invasive *P. australis* lineages have more positive PSFs than the native lineage; (2) indirect spillover and soil legacies of soil biota on *S. alterniflora* are more negative from invasive than native *P. australis* lineages; (3) the direction and strength of PSFs, spillover, and soil legacies depend upon the presence of an interspecific competitor and nutrient availability; (4) invasive *P. australis* lineages exhibit stronger interspecific competitive ability and response to nutrient availability than native lineages and *S. alterniflora*; and (5)

TABLE 1. Two-way interactions of interest between the soil inoculum treatment and other explanatory variables, with possible biological interpretations and observed experimental outcomes for *Phragmites australis* and *Spartina alterniflora*.

Interaction	Plant species	Interpretation	Observed
S × L	*P. australis*	A more positive impact of soil biota from native than invasive *P. australis* would indicate biotic resistance, whereas the opposite would suggest enemy release is occurring.	No interaction.
S × L	*S. alterniflora*	A more positive impact of soil biota from the native than invasive *P. australis* lineage on *S. alterniflora* would indicate negative spillover (apparent competition) from invasive *P. australis* lineages. The opposite would suggest facilitation (apparent mutualism) by invasive *P. australis*.	Negative spillover from invasive lineages, positive spillover from native lineages.
S × C	*P. australis*	The impact of soil biota on *P. australis* is altered by the presence of *S. alterniflora*. Soil biota change the impact of interspecific competition	Soil biota and competition had synergistic negative impacts.
S × C	*S. alterniflora*	The impact of soil legacies (with *P. australis* not present) differ from that of spillover (when *P. australis* is present). Soil biota alter the impact of interspecific competition.	Soil legacy impact was more negative than soil biota spillover. Soil biota attenuated competition via interactions with nutrient availability.
S × N	both	Nutrient availability influences direct and indirect impacts of soil biota and soil biota alter plant responses to nutrient availability.	Soil biota increased *P. australis* response to nutrients. Soil biota had decreased impact on *S. alterniflora* under low nutrient availability and weakened the difference in nutrient effects between competition treatments.

Note: Explanatory variables are *P. australis* lineage (L; native, European, Gulf), presence/absence of an interspecific competitor (C), high/low nutrient availability (N), and live/sterile soil inoculum (S).

nutrient availability and lineage-specific PSFs alter interspecific competition between *P. australis* and *S. alterniflora*.

MATERIALS AND METHODS

Study organisms

Phragmites australis is a model organism for studying plant invasions (Meyerson et al. 2016) and one of the most widely distributed plants in the world. Multiple genetic lineages of *P. australis* grow sympatrically in North America (Saltonstall 2002, Meyerson et al. 2009, 2012, Lambertini et al. 2012, Meyerson and Cronin 2013). The native lineage is endemic to North America and consists of at least 14 different haplotypes (Saltonstall 2002, Meadows and Saltonstall 2007). An invasive lineage of *P. australis* from Europe has spread aggressively in wetlands of North America since first appearing in herbarium records ~150 years ago (Saltonstall 2002, Howard et al. 2008, Meyerson et al. 2012). This invasive European lineage is mostly composed of a single haplotype (*M*) and forms large, dense, monospecific populations that negatively impact hydrology, native plant diversity, habitat quality for fauna, and ecosystem function (reviewed by Meyerson et al. 2009). An additional lineage (known as Gulf) is widely distributed along the Gulf of Mexico and west to California (Lambertini et al. 2012, Meyerson et al. 2012) and is likely a recent arrival from Mexico or Central America (Colin and Eguiarte 2016). Although its mode of introduction to North America remains unknown, we classify it as invasive (following Richardson et al. 2000) due to its fast-growing populations (Bhattarai and Cronin 2014) and rapid spread (Meyerson et al. 2012).

Recent studies with *P. australis* have described distinct oomycete, archaea, and bacteria communities from rhizosphere soil of native and European *P. australis* lineages in North America (Nelson and Karp 2013, Crocker et al. 2015, Yarwood et al. 2016, Bowen et al. 2017). Divergent community structure of soil biota suggests the direction and magnitude of PSFs may also differ among *P. australis* lineages, but this has yet to be assessed experimentally. The exceptions are the studies by Crocker et al. (2015, 2017), which demonstrated that various *Pythium* oomycetes differed in their virulence to seedlings of several wetland plant species based on the *P. australis* lineage they were isolated from (Crocker et al. 2015), whereas the impact of bulk soil did not differ between lineages (Crocker et al. 2017). However, these studies focused on seedling survival and did not investigate other fitness-related traits such as growth (i.e., biomass). Furthermore, the ecology, trophic interactions, and microbial community of the Gulf lineage remains virtually unknown (but see Bowen et al. 2017).

The widely distributed perennial grass *S. alterniflora* is native to salt marshes on the East and Gulf Coasts of North America, but invasive in other locations, such as the West Coast of North America (Tyler et al. 2007) and China (Zhao et al. 2010, Li et al. 2014). We selected *S. alterniflora* as a standardized competitor because it is a dominant plant in many coastal marshes, where it co-occurs with *P. australis* (Bertness 1991, Medeiros et al. 2013) and even shares pathogens (Li et al. 2014). The response to abiotic factors and competitive ability of *S. alterniflora* have been well described; specifically, *S. alterniflora* has a strong positive response to increased nutrient availability (Tyler et al. 2007, Zhao et al. 2010) and is generally an inferior competitor to *P. australis* and other salt marsh plants, except in environments with high abiotic stress (Bertness 1991, Pennings et al. 2005, Medeiros et al. 2013).

Greenhouse experiment design

We conducted a greenhouse experiment to examine the interactive effects of soil biota, interspecific competition, and nutrient availability on clonal growth (i.e., above- and belowground biomass) of the three *P. australis* lineages in North America and native *S. alterniflora*. The experimental design consisted of four treatments: (1) Live/sterile soil biota. Live or sterilized soil inoculum collected in situ from the rhizosphere of each *P. australis* population was added to each pot (10% of total soil mass to minimize variation in abiotic soil properties and nutrient flushes following soil sterilization). Soil biota was always combined with its associated *P. australis* population such that no mixing of soil and *P. australis* sources occurred. (2) Presence/absence of an interspecific competitor. Pots were planted with either *P. australis, S. alterniflora*, or both species combined. (3) High/low nutrient levels. Nutrient levels were manipulated to represent nutrient-rich and nutrient-poor environments. (4) *P. australis* lineage. Plants and corresponding soil inoculum from populations of the native, European, and Gulf lineages of *P. australis* were used for the experiment. These four treatments were fully crossed (36 total treatment combinations) and replicated among clones from three distinct *P. australis* populations within each lineage (Table 2). Individuals within each population were clones propagated from rhizome cuttings and populations were selected to represent a broad geographic distribution of the three main *P. australis* lineages in North America. We planted 10 replicates of each of the treatment combinations for all nine *P. australis* populations, resulting in a total of 1,080 pots. Planting was staggered over a six-week period during 1 April to 12 May 2015 because of the travel required to collect bulk soil, the large number of replicates, and the replacement of some rhizomes and plugs that did not establish successfully. Plants were grown in a greenhouse located at Louisiana State University (30.36° N, 91.14° W) and pots were arranged in a randomized blocked design with five blocks to account for possible gradients in the greenhouse environment. Due to the fast growth rate of *P. australis* and *S. alterniflora* and the relatively small pot size used, we anticipated that pot-binding of roots could limit biomass production (Poorter et al. 2012), which may make testing for effects on biomass conservative. A more detailed description of the experimental treatments and design is provided in Appendix S1.

Data collection and analysis

Harvesting was completed from 5 to 13 December, 2015. At this southern climate, plants were still growing and had not reached the flowering stage, which generally follows the second year of growth when propagating from rhizome cuttings. Above- and belowground biomass was harvested for each plant species from each pot, oven-dried to constant mass at 60°C, and weighed to the nearest 0.1 g. Because no plants produced a panicle, we used above- and belowground biomass (i.e., clonal growth) and root : shoot ratio (i.e., biomass allocation) as fitness proxies. As these variables all demonstrated similar results, we focus on total biomass for our results and discussion, but report fully on these other variables in Appendices S2, S3, and S4.

To examine how response variables for each plant species (*P. australis*, *S. alterniflora*) were influenced by *P. australis* lineage (native, European, Gulf), live/sterile soil inoculum, presence/absence of an interspecific competitor, and high/low nutrient availability, we used Akaike's Information Criteria corrected for finite sample size (AIC_c) to select the most informative mixed-effect model from a set of candidate models (Burnham and Anderson 2010). The full model included the variables above and all two-, three-, and four-way interactions as fixed effects (15 total variables). *Phragmites australis* population (nested within lineage) and greenhouse block were included as random effects to account for within-lineage variation and possible greenhouse environment gradients, respectively. We report AIC_c weights that indicate the proportional strength of support for model *i* being the best model given the set of plausible models ($\Delta\text{AIC}_\text{c} \leq 2$). For our interpretations, we estimated least-squares means (back-transformed) based on the most likely model for each response variable and focused on reporting effect sizes (i.e., proportional differences in means; Burnham and Anderson 2010, Ellison et al. 2014). For brevity, we focus the results and discussion on the interesting yet poorly understood interaction effects (see Table 1).

RESULTS

Which factors influence growth of Phragmites australis *and* Spartina alterniflora*?*

Soil inoculum, interspecific competition, nutrient availability, and their two-way interactions were identified as influential in explaining variation in *P. australis* total biomass using AIC_c model selection. Four candidate models received adequate support ($\Delta\text{AIC}_\text{c} \leq 2$) and all included the three main effects (cumulative AIC_c weight = 1) and various interactions between them. The top model (AIC_c weight = 0.429, Table 3) included the main effects only and had two times the support of the other three plausible models (second top model: AIC_c weight = 0.218). The second, third, and fourth models contained the interspecific competition × soil inoculum, nutrient availability × soil inoculum, and interspecific competition × nutrient availability interaction terms, respectively. For *S. alterniflora*, the variables influential in explaining biomass were: *P. australis* lineage, soil inoculum, interspecific competition, nutrient availability, and the lineage × soil inoculum, lineage × nutrient availability, interspecific competition × soil inoculum, and interspecific competition × nutrient availability interactions (top model, AIC_c weight = 0.714, Table 3). The second top model (AIC_c weight = 0.286) also included these variables plus the nutrient availability × soil inoculum and interspecific competition × nutrient availability × soil inoculum interactions but had less than half the support of the top model. The top models for other *P. australis* and *S. alterniflora* response variables (aboveground biomass, belowground biomass, root : shoot ratio; see Appendices S2, S3, and S4) were remarkably similar to those for total biomass. However, lineage-specific effects were more prevalent and three additional terms were identified as influential: the lineage × soil inoculum interaction for *P. australis* aboveground biomass, the lineage × nutrient availability interaction for *P. australis* root : shoot ratio, and the lineage × interspecific competition × soil inoculum interaction for *S. alterniflora* root : shoot ratio.

Do direct and indirect PSFs vary among Phragmites australis *lineages?*

Based on the top model, live soil biota had a consistently negative impact on *P. australis*, reducing biomass by 10% across all treatments, regardless of the *P. australis* lineage (i.e., no interactions with lineage in the four selected models). In contrast, the direction of the impact of *P. australis* soil inoculum on *S. alterniflora* biomass depended on the *P. australis* lineage the soil inoculum was sourced from (lineage × soil inoculum interaction). The impact of soil biota on *S. alterniflora* biomass was negative for invasive (a 7% decrease relative to sterile soil; European, 23.33 ± 0.06 g to 20.30 ± 0.06 g [mean ± SE]; Gulf, 23.78 ± 0.06 g to 20.68 ± 0.06 g) but positive for native (a 6% increase from 18.14 ± 0.06 g to 20.44 ± 0.06 g) *P. australis* lineages, an overall difference in biomass of 13% (Fig. 1).

Do PSFs depend upon competition and nutrient availability?

PSFs for *P. australis* were altered by the presence of *S. alterniflora* as a competitor (interspecific competition × soil

TABLE 2. List of *Phragmites australis* field populations used for the greenhouse experiment.

Population name, state (ID code)	Latitude (°N)	Longitude (°W)	Lineage	Status
Palm Canyon Road, California (PCN)	33.83	116.62	native	endemic
Little Caliente Hot Springs, California (LCN)	34.54	119.62	native	endemic
Mackay Island, North Carolina (NCN)	36.51	75.95	native	endemic
East Cameron, Louisiana (ECM)	29.77	93.29	European	invasive
I-40, Arizona (I40M)	34.72	114.49	European	invasive
Mackay Island, North Carolina (NCM)	36.51	75.95	European	invasive
Okeeheelee Park, Florida (FLI)	26.65	80.16	Gulf	invasive
Intracoastal City, Louisiana (ICI)	29.78	92.20	Gulf	invasive
Creole, Louisiana (CRI)	29.83	93.11	Gulf	invasive

inoculum interaction) and nutrient availability (nutrient availability × soil inoculum interaction). When grown alone, *P. australis* biomass was 7% lower in pots with live (47.51 ± 0.52 g) than pots with sterile (51.12 ± 0.52 g) soil inoculum (Fig. 2A), whereas the negative impact of soil biota was twofold higher (14%) on *P. australis* biomass when *P. australis* was grown with *S. alterniflora*, (live: 39.54 ± 0.52 g, sterile: 46.03 ± 0.52 g). In nutrient-poor pots, *P. australis* had 10% lower biomass in live (29.67 ± 0.52 g) than sterile (32.91 ± 0.52 g) soil inoculum (Fig. 2B). A slightly higher impact of 11% (live 59.88 ± 0.52 g, sterile 67.06 ± 0.52 g) was observed in the nutrient-rich treatment. Interestingly, the direction of the impact of *P. australis* soil inoculum on *S. alterniflora* biomass depended on a three-way interaction with interspecific competition and nutrient availability (interspecific competition × nutrient availability × soil inoculum interaction). When grown alone and under high nutrients, *S. alterniflora* biomass was 14% lower in pots with live (44.04 ± 0.05 g) than sterile (50.92 ± 0.05 g) *P. australis* soil inoculum (Fig. 3). Conversely, when competing with *P. australis* under the high nutrient treatment, *S. alterniflora* plants in live soil inoculum had 13% higher biomass (21.05 ± 0.05 g) than those in sterile inoculum (18.69 ± 0.05 g), a 27% difference between the competition treatments. Under low nutrient conditions, live soil inoculum from *P. australis* decreased *S. alterniflora* biomass by 10% (from 18.32 ± 0.05 g to 16.51 ± 0.05 g) and 5% (from 8.27 ± 0.05 g to 7.82 ± 0.05 g) when alone and competing with *P. australis*, respectively.

Do PSFs alter competition and interact with nutrient availability?

Soil inoculum and nutrient availability both altered the impact that interspecific competition with *S. alterniflora* had on *P. australis* biomass. Competition with *S. alterniflora* decreased biomass of *P. australis* by 17% in live soil inoculum pots and 10% in sterile soil inoculum pots (means and standard error presented in previous section; Fig. 2A). The effect of nutrient availability was small: competition decreased *P. australis* biomass by 13% (from 67.88 ± 0.52 g to 59.07 ± 0.52 g) in nutrient-rich pots and 14% (from 33.65 ± 0.52 g to 28.99 ± 0.52 g) in nutrient-poor pots (Fig. 4). For *S. alterniflora*, interspecific competition with *P. australis* decreased biomass by 63% when grown in sterile soil inoculum and under the nutrient-rich treatment, compared to 52% in live soil inoculum (means and standard error presented in previous section; Fig. 3). This difference between soil inoculum treatments was less pronounced when nutrients were limited, where competition decreased biomass by 55% and 53% in sterile and live soil pots, respectively.

Increased nutrient availability doubled *P. australis* biomass, which was 104% and 102% higher than in nutrient-poor pots when grown alone and with *S. alterniflora* as a competitor, respectively (means and standard error presented in previous section; Fig. 4). A similar impact of higher nutrient availability occurred in live soil inoculum (a 102% increase in biomass; means and standard error presented in previous section), although only a 73% increase was observed in sterile soil inoculum (Fig. 2B). Increased nutrient availability also had a strong effect on *S. alterniflora* biomass via a combined interaction with soil inoculum and interspecific competition. In sterile soil inoculum, biomass was 178% and 126% higher in nutrient-rich than nutrient-poor pots when grown alone and with *P. australis* as a competitor, respectively (means and standard error presented in previous section; Fig. 3). However, when grown with live soil inoculum, higher nutrient availability increased *S. alterniflora* biomass by similar quantities of 167% when grown alone and 169% when competing with *P. australis.* Finally, in nutrient-poor pots, differences in *S. alterniflora* biomass among pots with soil inoculum from different *P. australis* lineages were relatively small (<4%, range of 12.10 to 12.53 ± 0.06 g, Fig. 5). However, in nutrient-rich pots, *S. alterniflora* grown with soil inoculum from the invasive lineages of *P. australis* had 19% higher biomass (European, 34.30 ± 0.06 g; Gulf, 34.62 ± 0.06 g) than pots with soil inoculum or plants from the native lineage

TABLE 3. Akaike's Information Criteria corrected for finite sample size (AIC$_c$) best models (ΔAIC$_c \le 2$) explaining variation in total biomass (square-root transformed) for each plant species (*Phragmites australis* or *Spartina alterniflora*).

Response variables	Models	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
Phragmites australis total biomass				
C, N, S		2,611.6	0.00	0.429
C, N, S, C × S		2,612.9	1.35	0.218
C, N, S, N × S		2,613.3	1.73	0.181
C, N, S, C × N		2,613.4	1.82	0.173
Spartina alterniflora total biomass				
C, L, N, S, C × N, C × S, L × N, L × S		2,373.5	0.00	0.714
C, L, N, S, C × N, C × S, L × N, L × S, N × S, C × N × S		2,375.4	1.83	0.286

Note: Explanatory variables are as in Table 1.

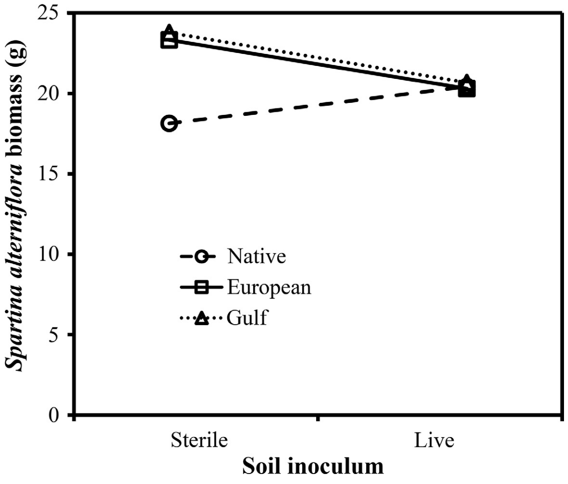

FIG. 1. Indirect impact of live or sterilized soil inoculum obtained from the three *Phragmites australis* lineages on biomass (g; least squares mean ± SE) of *Spartina alterniflora*. The interaction between soil inoculum and *P. australis* lineage was identified as influential using mixed-effects model selection (see Table 3). Error bars obscured due to small size; n = 109–114.

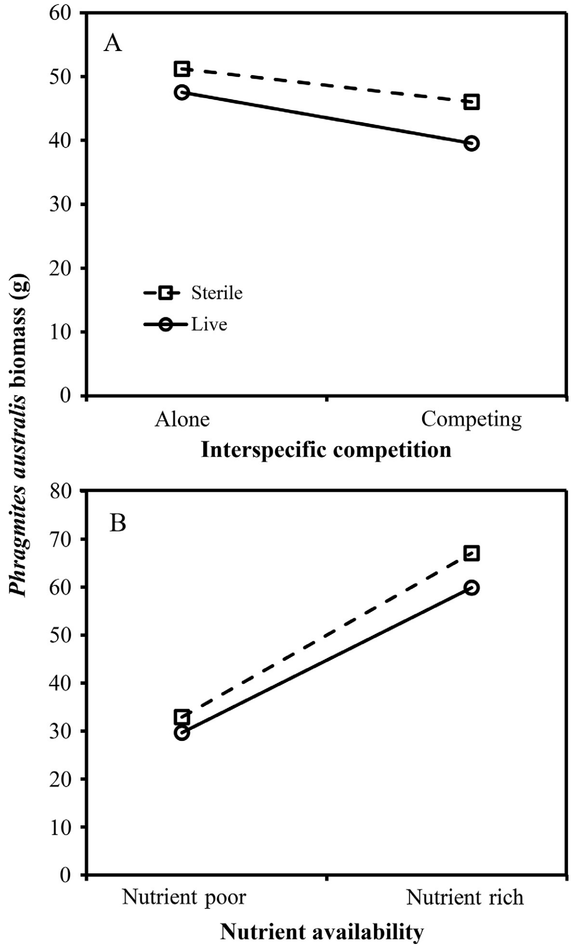

FIG. 2. Interactive effects of live or sterilized soil inoculum with (A) presence/absence of competition with *Spartina alterniflora* and (B) low or high nutrient availability on biomass (g; least squares mean ± SE) of *Phragmites australis*, identified as influential using mixed-effect model selection (see Table 3). Error bars obscured due to small size; n = 148–177.

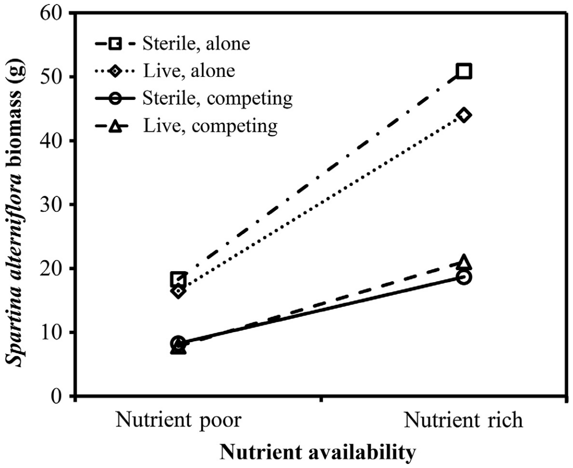

FIG. 3. Interactive effects of live or sterilized soil inoculum with the presence/absence of competition with *Phragmites australis* and low or high nutrient availability on biomass (g; least squares mean ± SE) of *Spartina alterniflora*, identified as influential using mixed-effect model selection (see Table 3). Error bars obscured due to small size; n = 70–97.

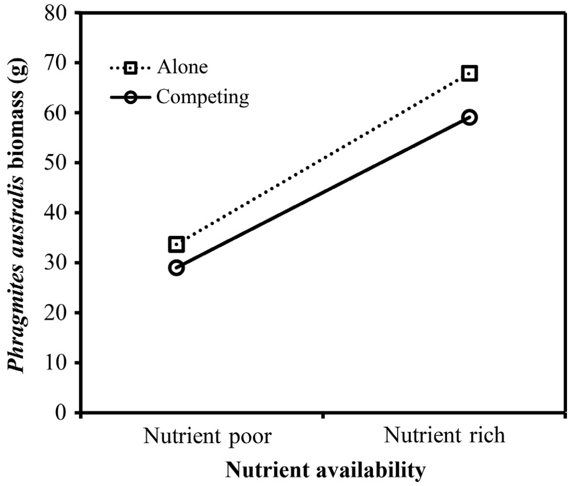

FIG. 4. Interactive effect of presence/absence of competition with *Spartina alterniflora* and low or high nutrient availability on biomass (g; least squares mean ± SE) of *Phragmites australis*, identified as influential using mixed-effect model selection (see Table 3). Error bars obscured due to small size; n = 145–170.

(27.89 ± 0.06 g) (lineage × nutrient availability interaction). This pattern was consistent regardless of the presence of *P. australis* as a competitor or whether the soil inoculum was live or sterile.

DISCUSSION

The consistent negative impact of soil biota observed for all *P. australis* lineages supports the established view that conspecific PSFs are predominantly negative (Bever 2003, Kulmatiski et al. 2008) and suggests that interactions with soil biota do not directly influence the success of invasive *P. australis* lineages. In contrast, biomass of native *S. alterniflora* was reduced by indirect PSFs involving soil biota from invasive *P. australis* populations, whereas soil biota from native *P. australis* populations had a positive effect, suggesting the potential to exclude and facilitate co-occurring native plant species, respectively (Bever et al. 1997, Klironomos 2002, van der Putten et al. 2013). Interestingly, PSFs involving *P. australis* soil biota were negative for *S. alterniflora* grown alone (i.e., a negative soil legacy) but positive when grown in the presence of *P. australis*, suggesting that *P. australis* may be preferred by harmful generalist soil biota, or facilitates *S. alterniflora* via apparent mutualism. To our knowledge, this is the first study to demonstrate that the direction of indirect PSFs differs among conspecific native and invasive plant taxa and can change depending upon the presence/absence of the initial host plant of the soil biota (i.e., between spillover and soil legacy). Consistent with previous studies (Bertness 1991, Pennings et al. 2005), we also found *P. australis* to be a dominant interspecific competitor and that *S. alterniflora* had a stronger response to increased nutrient availability, which mediated the impact of interspecific competition on *S. alterniflora*. Contrary to expectations, we found little support for the hypothesis that invasive *P. australis* lineages have superior interspecific competitive ability or response to nutrients when compared to the native lineage. Taken together, our results suggest that intraspecific variation in indirect PSFs (i.e., spillover and soil legacies) may play an underappreciated role in influencing plant invasions, including *P. australis* in North America, and that their importance is greater than that of direct PSFs, which lack intraspecific variation and context dependency. Our study integrates multiple factors linked to invasion success, highlights how indirect interactions can underpin successful invasions and their impact, and could inform approaches to management and restoration of areas invaded by *P. australis.*

Direct PSFs of Phragmites australis *lack intraspecific variation*

Contrary to previous studies (Klironomos 2002, Agrawal et al. 2005, Kulmatiski et al. 2008, Suding et al. 2013, but see Callaway et al. 2013) and our first prediction, invasive *P. australis* lineages do not benefit from more positive PSFs than the native lineage, indicating that soil biota does not directly facilitate the relative success of invasive *P. australis* lineages in North America. This unexpected result is consistent with that of Bowen et al. (2017), who used structural equation modeling to infer that rhizosphere bacterial richness, activity, and metabolism did not mediate *P. australis* biomass. One possible reason for the lack of differences in PSF strength among lineages could simply be that although lineages differ in their microbial communities, their net effects on the plant are the same. However, studies in other systems contradict this explanation, such as that of Wagg et al. (2015) who demonstrated that differences in PSFs of two populations of *Trifolium pratense* were related to corresponding differences in the rhizosphere microbe community. Finally, it is important to note that our estimated effect sizes of PSFs on biomass are likely conservative due to the use of a small soil inoculum (10% total soil weight), and these effects may intensify with a larger inoculum volume.

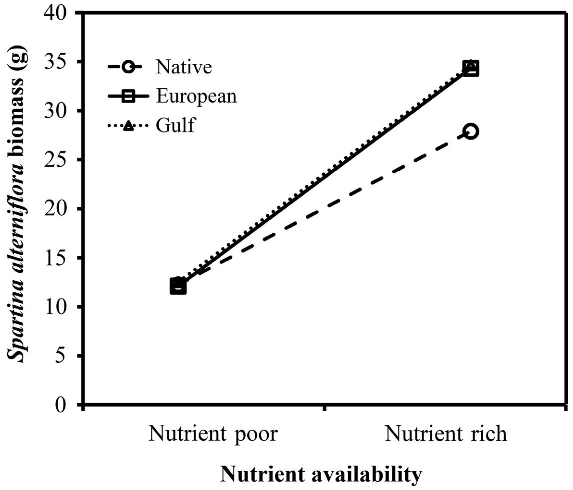

FIG. 5. Interactive effects of low or high nutrient availability with soil inoculum from the three *Phragmites australis* lineages on biomass (g; least squares mean ± SE) of *Spartina alterniflora,* identified as influential using mixed-effect model selection (see Table 3). Error bars obscured due to small size; n = 103–118.

Lineage-specific PSFs promote invasion through indirect effects on Spartina alterniflora

In support of our second prediction, we found that generalist rhizosphere soil biota from the two invasive *P. australis* lineages had a net negative impact on *S. alterniflora* biomass, whereas soil biota from the native lineage had a net positive impact (lineage × soil inoculum interaction). This finding contrasts with the recent study by Crocker et al. (2017), which found that soils from the native and European lineages did not differ in their impact on seedlings of several native and invasive wetland plant species. The large extent and density of populations of the invasive *P. australis* lineages relative to the native lineage and other native wetland plants means that even small invasion-induced changes in PSFs could be widespread and important in invaded habitats. Thus, our study represents the first to demonstrate intraspecific variation in spillover and provides support for its importance as a potential mechanism driving plant invasions. One possible explanation for the negative impact on *S. alterniflora* could be that invasive *P. australis* accumulates local generalist soil pathogens, which spillover onto *S. alterniflora*, overwhelming any positive impacts from beneficial organisms (Borer et al. 2007, Mangla et al. 2008). Similarly, beneficial soil biota may spillover to *S. alterniflora* from soil associated with the native *P. australis* lineage, representing a possible explanation for why the native *P. australis* lineage usually co-occurs with a diverse suite of other native species (Meyerson et al. 2009). These indirect interactions are representative of apparent competition and mutualism, respectively, whereby shared natural enemies or mutualists mediate interactions between two or more species. There is growing support for apparent competition involving herbivores and pathogens as an important driver of plant invasions (Borer et al. 2007, Dangremond et al. 2010), including for *P. australis* (Bhattarai et al. 2017*a*). Interestingly, Li et al. (2014) demonstrated pathogen spillover between *P. australis* and *S. alterniflora* in the Yangtze River estuary in China, but the roles of the species were reversed; there, *S. alterniflora* is invasive and spillover of the fungal pathogen *Fusarium palustre* was implicated in significant dieback of native *P. australis.*

Direct and indirect PSFs are altered by competition and nutrient availability

In support of our third prediction, indirect PSFs for *S. alterniflora* were more positive in the presence of *P. australis*, with the strongest effect observed in nutrient-rich pots (interspecific competition × nutrient availability × soil inoculum interaction). In comparison, competition with *S. alterniflora* had the opposite effect for *P. australis*, doubling the negative impact of its direct PSFs (interspecific competition × soil inoculum interaction), and with minimal interaction with nutrient availability. Intriguingly, our findings are similar to those of the only other study to take such a multi-factor approach to the role of PSFs in plant invasions, where Larios and Suding (2015) found that PSFs of native purple needlegrass (*Stipa pulchra*) exhibited stronger context dependency than invasive wild oat (*Avena fatua*). At least two scenarios could explain the effects we observed. First, harmful generalist soil biota may interact preferentially with *P. australis*, only switching hosts to *S. alterniflora* when *P. australis* is absent. Such a preference could be expected given that the soil inoculum was originally collected from naturally occurring *P. australis* populations and likely contained organisms co-adapted to that population, lineage, and species (Nelson and Karp 2013, Yarwood et al. 2016, Bowen et al. 2017). Thus, we suggest that *P. australis* generates a negative soil legacy whereby harmful generalist soil biota switch to native host species when *P. australis* is no longer present. Negative soil legacies appear to be relatively common among invasive species and are widely recognized to prevent establishment of native plants and improve chances of invader recolonization (D'Antonio and Meyerson 2002, Corbin and D'Antonio 2012, Grove et al. 2015). Second, our findings could be indicative of spillover of beneficial soil biota cultivated by *P. australis* to *S. alterniflora* (i.e., an apparent mutualism), indicating that *P. australis* may indirectly facilitate the growth of co-occurring native plants. This scenario is also supported by the twofold increase in strength of negative PSFs for *P. australis* when grown with a competitor, suggesting that beneficial soil biota preferentially interact with *S. alterniflora* when it is present, or the potential for a trade-off between investment in competition and pathogen defense for *P. australis.* Regardless, all of these possible underlying mechanisms cannot easily be disentangled without identifying the organisms involved or further experiments, which were outside the scope of this study.

Little intraspecific variation in the impacts and interaction of interspecific competition and nutrient availability

Superior competitive ability has long been recognized as a common trait of invasive plant species (Elton 1958, reviewed by Gioria and Osborne 2014) and is often cited as one of the main reasons the European *P. australis* lineage has become so prevalent in North America. In support of this view and our fourth prediction, we found that *P. australis* was a superior competitor to *S. alterniflora*. This result is consistent with studies showing that native *S. alterniflora* tends to be restricted to lower marsh areas due to its poor competitive ability but superior tolerance of abiotic stress factors such as high salinity and flooding (Bertness 1991, Pennings et al. 2005). Several studies have also indicated that European *P. australis* is a stronger competitor than the native and Gulf lineages (Howard et al. 2008, Holdredge et al. 2010). However, we failed to find any differences in total biomass, interspecific competitive ability, or impact on *S. alterniflora* biomass among the three *P. australis* lineages. Thus, we suggest that interspecific competitive ability may not be a key factor explaining the predominance of European relative to native and Gulf *P. australis* in North America.

Increased nutrient deposition via disturbance and anthropogenic modification is also often considered a major contributing factor to *P. australis* invasion success (Bertness et al. 2002, Holdredge et al. 2010) and plant invasions in general (Dukes and Mooney 1999). Unsurprisingly, nutrient availability had a strong effect on biomass of both our study species, but this was greater for *S. alterniflora* than *P. australis* (Zhao et al. 2010), which may help explain why *S. alterniflora* has become an invasive plant in salt marshes on the West Coast of North America (Tyler et al. 2007), China (Zhao et al. 2010, Li et al. 2014), and elsewhere. The lack of variation in nutrient effects among *P. australis* lineages could be considered surprising, given that European invasive *P. australis* enjoys a higher maximum nutrient uptake ability than the native lineage (Mozdzer et al. 2010). However, differences may be more subtle, such as the stronger plasticity in biomass allocation (root : shoot ratio) in response to nutrient addition that we observed for the European invasive lineage (see Appendix S3), which may impact other measures of fitness (i.e., sexual reproduction) or biomass over more than one growing season. Finally, despite being pot bound, we found strong effects of nutrients on plant biomass, suggesting that pot-binding did not inhibit our ability to detect other treatment effects.

Additionally, *S. alterniflora* grown in pots containing soil inoculum from the native *P. australis* lineage did not respond as positively to nutrient additions as plants associated with soil inoculum from the invasive *P. australis* lineages (lineage × nutrient availability interaction). This effect was independent of the presence of *P. australis* and soil biota sterilization, suggesting that abiotic factors of the original soil inoculum may have affected nutrient uptake of *S. alterniflora* in nutrient-rich pots, a surprising result given the low soil inoculum ratio of 10% of total soil mass. Furthermore, interspecific competition had minimal impact on the response of *P. australis* to changes in nutrient availability (interspecific competition × nutrient availability interaction), but *S. alterniflora* biomass increase in response to nutrients was highest when grown on its own. This result is unsurprising, given that *P. australis* is the superior competitor and its presence should reduce the ability of *S. alterniflora* to fully utilize resources. However, live soil biota all but eliminated this interaction for *S. alterniflora*, suggesting that PSFs indirectly attenuate competitive effects on the ability of *S. alterniflora* to respond to increased nutrient availability. This result could also be expected, considering the consistently negative impact of PSFs on *P. australis* that was twice as strong when competing with *S. alterniflora*. Interestingly, *P. australis* responded more strongly to added nutrients in live than sterile soil, indicating that the negative impact of soil biota on *P. australis* may be countered by an increased response to added nutrients via soil mutualists. Perhaps most importantly, these effects did not vary among *P. australis* lineages, and taken together, our results suggest that nutrient deposition may not directly contribute to the spread of invasive *P. P. australis* lineages into wetlands and marshes dominated by native *P. australis* or *S. alterniflora*.

Nutrient availability and PSFs alter the impact of interspecific competition

Several studies have found that soil biota and nutrient availability can significantly alter the outcome of interspecific competition (Casper and Jackson 1997, Casper and Castelli 2007, Hodge and Fitter 2013, but see Maron et al. 2016). In support of these previous studies and our fifth prediction, we found that both PSFs and nutrient-poor conditions reduced the negative impact of interspecific competition on biomass of *S. alterniflora*, yet the opposite effects were observed for *P. australis* (nutrient availability × soil inoculum and interspecific competition × nutrient availability interactions). The effect of soil biota on interspecific competition can likely be attributed to the consistent negative PSF suffered by *P. australis,* which may decrease its competitive ability or strengthen the beneficial spillover affecting *S. alterniflora*. Moreover, our findings contrast with earlier studies that found nutrient addition reduces negative impacts of interspecific competition on *S. alterniflora* (Levine et al. 1998, Emery et al. 2001). However, these experiments did not use *P. australis* as a competitor, a species possessing one of the highest nitrogen use efficiencies of all land plants (Mozdzer et al. 2013). Furthermore, at high levels of nutrient availability, light becomes the main limiting resource in plant competition (Casper and Jackson 1997, Aerts 1999), meaning that the taller *P. australis* would continue to outcompete the shorter *S. alterniflora*. Moreover, no differences in the impact of these competitive interactions on *S. alterniflora* total biomass were detected among *P. australis* lineages, indicating they are unlikely to be influential in explaining the relative success of invasive versus native *P. australis* lineages in North America.

Future directions

The identity and impact of the soil community should be an important consideration when attempting to restore habitat occupied by invasive plant species (D'Antonio and Meyerson 2002, Corbin and D'Antonio 2012). Thus, we suggest that future studies should focus on the identification of lineage-specific pathogens and mutualists that may be useful in novel management efforts with the goal of controlling invasive *P. australis* lineages and restoring the native lineage, respectively (Kowalski et al. 2015). Because invasive species interact directly and indirectly with a complex community of organisms and abiotic conditions, expanding PSF studies to multitrophic and community level interactions, and continuing to address context dependency, is critical to furthering our understanding of the role of PSFs in plant invasions. Moreover, our understanding of the general role of PSFs in community ecology remains limited. Insights into the eco-evolutionary dynamics of PSFs (terHorst and Zee 2016), how single-species greenhouse experiments translate to the community level and field observations, and continuing to open the PSF "black box" through identifying key taxa and their functions, promise to remain fruitful research areas for many years to come.

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SUPPORTING INFORMATION

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