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Invasive grasses consistently create similar plant–soil feedback types in soils collected from geographically distant locations

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Abstract

Aims
Plants of similar life forms and closely related species have been observed to create similar types of plant–soil feedbacks (PSFs). However, investigations of the consistency of PSFs within species have not yielded clear results. For example, it has been reported that species create different types of PSFs in their native and introduced ranges. The aim of this project is to examine if four species create similar PSF types from soils collected from widely distributed areas within their introduced range. The soil for this project was collected from three areas in western North America. With this design, we aim to determine species- and site-specific ability to create PSFs and if the type of PSF created is consistent in all soil from all three collection areas. The species examined are *Agropyron cristatum*, *Centaurea solstitialis, Poa pratensis* and *Taeniatherum caput-medusae*.

Methods
We used three-field collected soils (from northern Nevada, western Montana and eastern Montana) in a two-phase greenhouse experiment to quantify the type of PSFs created by four invasive species. The first phase was a conditioning phase wherein each invasive species created species-specific changes to the soil. The second phase of the experiment was the response phase wherein both the conditioning species and a native phytometer were grown in the conditioned soil and in unconditioned (control) soil. The final aboveground biomass was used to evaluate the effect of conditioning and to determine the type of PSF created by each invasive species.

Important Findings
Our results suggest that three of our four study species did show consistency in relation to PSF. Two species *A. cristatum* and *T. caput-medusae* consistently created PSF types that benefit conspecifics more than heterospecifics (and thus are ‘invasive’ PSF types) and *P. pratensis* consistently exhibited no, or ‘neutral’, feedbacks. The fourth species (*C. solstitialis*) was inconsistent: in one soil, no feedback was created; in other soil, an invasive PSF was created and in the last soil, a feedback that relatively benefited the native phytometer was created. Thus, PSFs appear to uniformly contribute to the success of two species (*A. cristatum* and *T. caput-medusae*) but not C. *solstitialis* nor *P. pratensis.*

Keywords: plant–soil feedback, invasion, niche construction

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INTRODUCTION

Plant–soil feedback (PSF) is one form of ecosystem engineering (Jones *et al.* 1994) wherein plants modify their environment in a manner that affects subsequent plant performance. Creating PSF is a two-step process. The first step is alteration of the soil environment by plants (‘soil conditioning’; Bever *et al.* 1997). During growth, plants actively alter both soil nutrients and the soil microbial community (Bever *et al.* 2013; Johnson *et al.* 2007; Jordan *et al.* 2012; Kourtev *et al.* 2003; Perkins *et al.* 2011; Wardle *et al.* 2004). The second step is the response of the subsequent generation of plants to this soil conditioning (Bever *et al.* 1997). Creating a favorable PSF results in greater invasive potential by increasing individual performance, population growth and/or competitive ability (Cuddington and Hastings 2004; Kylafis and Loreau 2008; Perkins and Nowak 2012). The PSF Hypothesis of Invasion asserts that a plant species with the ability to modify its soil environment in a manner that increases subsequent conspecific performance more than heterospecific performance is more invasive than species without that ability (Bever *et al.* 2010; Levine *et al.* 2006; Suding *et al.* 2013).

Of the five potential types of PSF (conspecific negative, heterospecific negative, conspecific positive, heterospecific positive and neutral), only two (conspecific positive and heterospecific negative) allow a plant to gain advantage within the recipient community and can be considered 'invasive PSF types' (Fig. 1). Theoretical frameworks (Bever *et al.* 1997) and empirical evidence (Perkins and Nowak 2013) suggest that many plant species exhibit negative feedbacks by altering soil conditions in a manner that decrease subsequent performance (e.g. plants in the next generation are smaller than plants in the conditioning generation). However, the response of subsequent generation may depend on species identity. A conspecific negative feedback occurs when the species that conditioned the soil incur a larger negative response than other species and a heterospecific negative feedback occurs when other species experience a larger negative response than the species that conditioned the soil. Some species alter soil conditions in a manner that increase subsequent plant growth (Klironomos 2002) creating positive PSF types. This increase in growth of the subsequent community can be species-specific; a heterospecific positive feedback occurs when other species experience a larger positive response compared to the species that conditioned the soil and a conspecific positive feedback occurs when the species that conditioned the soil has the largest positive response (Fig. 1). Some changes in soil conditions result in no growth differences in subsequent communities (i.e. plants create a neutral feedback). For example, *Ranunculus repens* (Harrison and Bardgett 2010) has been observed to significantly affect soil characteristics, but not in a manner that influenced growth of subsequent generations. Thus, despite the altered soil conditions (step 1 occurred), a neutral PSF was created because the changes in the soil did not affect subsequent plant growth (step 2 did not occur).

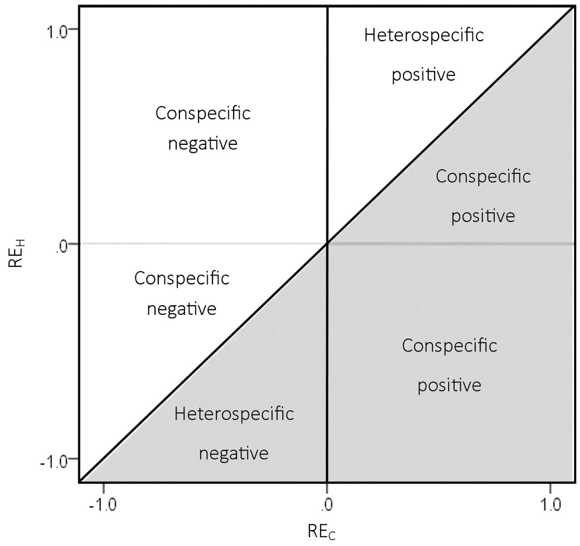

Figure 1: diagram of four potential PSF types from Perkins and Nowak (2013b) in the two-dimensional space of RE values.

$$\mathrm{RE} = \frac{\left((b_c) - (b_u)\right)}{\left((b_c) + (b_u)\right)}$$

where b the biomass of either the heterospecific (for the $\mathrm{RE_H}$ calculation) or the conspecific (for the $\mathrm{RE_C}$ calculation) in conditioned (b_c) or unconditioned (b_u) soils. A positive RE value indicates that a species produced more biomass in the conditioned soil compared to unconditioned soil, and a negative value indicates that a species produced less biomass in the conditioned soil compared to the unconditioned soil. The shaded gray area indicates invasive PSF types.

Accumulating evidence suggests interspecific consistency in PSF creation exists; e.g. plants of similar life forms (e.g. grasses) create similar types of PSF (Meisner *et al.* 2014) as do closely related species (Anacker *et al.* 2014). However, intraspecific consistency in PSF creation has not been observed. Both different accessions and different populations of a single species create different types of PSF (Bukowski and Petermann 2014; Felker-Quinn *et al.* 2011). Plants have been observed to create different PSFs in soils collected from extremely distant locations, generally native and invasive ranges (Gundale *et al.* 2014; Maron *et al.* 2014). For example, *Pinus contorta* did not create the same PSF in soils collected in western Canada (native range) and Sweden (invaded range, Gundale *et al.* 2014), nor did a suite of six invasive species create consistent PSFs in soils collected in Europe (native ranges) and North America (invaded ranges, Maron *et al.* 2014). The difference in type of PSF created between home ranges and invasive ranges has been interpreted to suggest that PSFs may contribute to biological invasions and habitat invasibility (Maron *et al.* 2014; Zuppinger-Dingley *et al.* 2011). Building on this, we question the consistency in PSF created by a single species when soils differ. To further test the species and site specificity of PSF, we suggest that invasive type PSFs may be consistently created within the invaded range. Some evidence is available that supports this suggestion. For example, three of four invasive species created consistent PSF types in two geographically close but distinct soil types within their invaded ranges (Perkins and Nowak 2013). Here, we extend this research to more geographically distant soils.

MATERIALS AND METHODS

In order to test PSF consistency, we grew four species invasive in North America in soils collected from three distinct geographically distant collection areas. We conducted a controlled environment experiment in a glasshouse in Reno, Nevada USA using soil collected from natural rangeland locations in northern Nevada (Area 1), western Montana (Area 2) and eastern Montana (Area 3). Soils were sieved to remove coarse fragments, homogenized and potted into SC10 Super pots (Stuewe and Sons, Corvallis, OR, USA). A sample of each soil was sent to Midwest Laboratories Inc., Omaha, NE, USA, for nutrient and textural analysis. For the duration of the experiment, glasshouse conditions were set to mimic outdoor conditions with diurnal temperature fluctuation between 7°C and 24°C and ambient light. Distilled water and careful and attentive watering were used to maintain pots near field capacity. Pots were frequently and randomly rearranged in the glasshouse to compensate for any environmental variation. The two-phase factorial experimental design (Fig. 2) included four invasive species (*Agropyron cristatum* (L.) Gaertn., *Centaurea solstitialis* L., *Poa pratensis* L. and *Taeniatherum caput-medusae* (L.) Nevski), soil from three areas either conditioned or unconditioned in the first phase (see below), and planted in the second phase with a 'response' species: either the species that conditioned the soil or a heterospecific native phytometer (four invasive species × three soils × two conditioning treatments × two response species). This entire design was replicated six times.

The two-phase experiment proceeded as follows. The first phase was the 'conditioning' generation wherein a first generation of invasive species was grown to induce species-specific changes in soil conditions. Several seeds were planted in each pot and seedlings were thinned to one plant per pot. A subset of pots was left unplanted but otherwise treated the same to provide unconditioned control soil. Soils were conditioned with the invasive species *A. cristatum, C. solstitialis, P. pratensis* or *T. caput-medusae.* After 80 days of the first phase, aboveground biomass of the conditioning plant was removed. Soil conditioned by a single species were then thoroughly mixed (to provide a homogenous treatment) within each replicate (to avoid pseudoreplication) and the soil was repotted. The second phase was immediately planted. These methods are similar to many other PSF experiments (Bever *et al.* 1997; Casper *et al.* 2008; Jordan *et al.* 2008; Kulmatiski *et al.* 2011; Perkins and Nowak 2012; Perkins and Nowak 2013). The second phase was the 'response' generation wherein a second generation of plants, either the conspecific conditioning species or a heterospecific native species common in all soil collection areas (*Koeleria macrantha* (Ledeb.) Schult.) was grown to assess the effects of soil conditions on subsequent plant growth. Hereafter we refer to *K. macrantha* as the phytometer species. Again, for the response generation, several seeds were planted per pot, pots were thinned to one seedling each, and pots with no establishment were reseeded at 7 days as needed. The response generation grew for 80 days after which the aboveground biomass was removed, dried for over 24 h at 70°C and weighed.

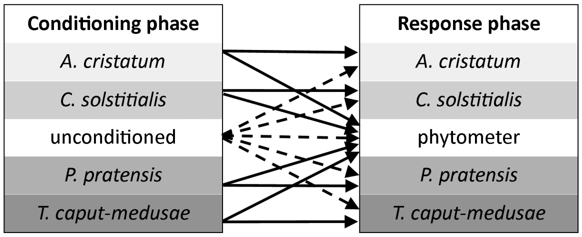

Figure 2: diagram of conditioning and response phase of the experiment. In the conditioning phase of the experiment, four invasive species were used to condition soil and some soil was left unplanted for an unconditioned control. In the response phase, each invasive species was grown in its own soil and in unconditioned soil. The phytometer was grown in every soil from the conditioning phase.

A relative effect (RE) index was calculated to examine the effect of PSF on the response generation while controlling for differences in soil fertility and resulting absolute plant size. The RE index is an adaptation of the R_{ii} index which has been used for plant interactions and has strong mathematical and statistical properties (i.e. it is symmetrical around zero, is linear and has no discontinuities in its range Armas *et al.* 2004; Brinkman *et al.* 2010). RE was calculated in each soil type conditioned by each invasive species for each response species separately using the following formula.

$$\mathrm{RE} = \frac{\left((b_c) - (b_u)\right)}{\left((b_c) + (b_u)\right)}$$

Where b_c is the biomass produced in the conditioned and b_u is the mean biomass produced in unconditioned soil. $\mathrm{RE_C}$ (RE conspecific) is the relative response of each invasive species to its own conditioned soil and $\mathrm{RE_H}$ (RE heterospecific) is the relative response of the phytometer. A positive RE value indicates that a species produced more biomass in the conditioned soil compared to unconditioned soil, and a negative value indicates that a species produced less biomass in the conditioned soil compared to the unconditioned soil.

Data were analyzed with JMP Pro 10 (JMP Pro, Version 10. SAS Institute Inc., Cary, NC,USA). Preliminary data analyses included boxplots to check for outliers and an assessment of homogeneity of variance. No data were excluded and the null hypothesis of homogeneous variances was not rejected at a 0.01 significance level for all soil and species combinations except for soil = Area 1 and species = *P. pratensis*. Analysis of variance (ANOVA) was used to test the effects of soil, species and their interaction. For ANOVA analysis with unbalanced data and two effects, least squares means are used to estimate population marginal means. Two sample *t* tests assuming unequal population variances were used to compare RE values to each other and to zero.

RESULTS

Soils from all three collection areas had different characteristics (Table 1) and soil collection area significantly impacted conspecific and phytometer biomass as well as $\mathrm{RE_H}$ but not $\mathrm{RE_C}$ (Table 2). Area 3 soil was relatively unproductive (Fig. 3). Generally, the invaders produced more biomass than the phytometer and cumulatively the most biomass was produced in Area 2 soil.

The identity of the conditioning species significantly affected conspecific biomass and native phytometer biomass as well as RE$_H$ and RE$_C$ (Table 2). In soil from all three collection areas conditioned by *A. cristatum* (Table 2, Fig. 4 triangles) RE$_C$ was greater than RE$_H$, consistent with invasive types PSF (Table 3). Thus, invasive PSF types were created by *A. cristatum* in all soils collected from its currently invaded range. RE values in soil conditioned by *C. solstitialis* tended to be negative, but there no consistent PSF type was created (Tables 2 and 3; Fig. 4 circles). Soils conditioned by *P. pratensis* never had an RE value significantly different from zero nor were RE$_H$ and RE$_C$ ever significantly different from each other (Table 2) thus *P. pratensis* always created neutral PSFs (Table 3). In soil conditioned by *T. caput-medusae*, RE$_H$ values were less than RE$_c$ values in the Areas 2 and 3 soil (Table 2; Fig. 4 squares). Despite replanting and careful tending, too few phytometer plants grew in Area 1 soil conditioned by *T. caput-medusae* for statistical analysis. Thus in soils from two collection areas, *T. caput-medusae* created invasive PSF types and if we consider failure to grow a decisive example of a negative PSF, invasive PSF types were created by *T. caput-medusae* in soils from all three areas (Table 3).

DISCUSSION

PSFs were consistent for three of the four species included in this study. *A. cristatum* and *T. caput-medusae* consistently created invasive PSF types in soils from three collection areas and *P. pratensis* consistently created neutral PSFs. *C. solstitialis* was the only species that was inconsistent, creating a neutral PSF, a conspecific negative feedback that would not contribute to invasion and a heterospecific negative feedback that is an invasive PSF type. These results suggest that PSF creation may uniformly contribute to the invasive potential of *A. cristatum* and *T. caput-medusae* but not *C. solstitialis* nor *P. pratensis*.

Conspecific negative PSF is the most commonly reported type of PSF (Bever *et al.* 1997; Kulmatiski *et al.* 2008). However, many PSF studies do not include heterospecific phytometers and only examine conspecific performance, which increases the probability of finding negative PSF (Kulmatiski *et al.* 2008). If we had only examined conspecific performance, we would have determined that *C. solstitialis, P. pratensis* and *T. caput-medusae* would have exhibited negative PSFs. However, it is the RE of the PSF on both conspecific and heterospecific performance that influences community dynamics and invasive potential. Thus, we included a heterospecific native phytometer species in our experiment. The impact of PSF on the growth of neighboring heterospecifics may have profound effects on plant community composition when vegetation dynamics are driven by competition (Tilman 1994) and ultimately influence population growth of invasive species (Cuddington and Hastings 2004). Phytometer species are often used as a common indicator for treatments in competition (Gaudet and Keddy 1995; Wardle *et al.* 1998), environmental gradient (e.g. nutrient limitation; Laliberte *et al.* 2012) and PSF (Bartelt-Ryser *et al.* 2005) experiments. Often studies use agricultural species as a phytometer. However, we chose *K. macrantha* as our native phytometer for three reasons: (i) because perennial grasses are the dominant life history form in the semiarid western US and are extremely economically important for livestock production; (ii) because *K. macrantha* is one of the few native perennial grass species that is common at all three sites and (iii) because *K. macrantha* is often used in revegetation where interference from invasive species can be strong (D'Antonio and Meyerson 2002). Further tests of the importance of PSF in facilitating invasion should improve upon this method by using multiple phytometer species, focus

Table 1: **soil properties of soil from each collection area prior to experimental soil conditioning**

	Area 1	Area 2	Area 3
Texture	Sandy loam	Sandy loam	Loam
pH	6.5	6.4	8.1
N (ppm NO_3-N)	7	14	4
P (ppm)	80	37	7
K (ppm)	216	274	181
Mg (ppm)	180	173	338
Ca (ppm)	1592	1740	2763
S (ppm)	9	9	60
Mn (ppm)	32	12	3
Fe (ppm)	54	39	11
Cu (ppm)	2.3	0.8	0.7

Table 2: **results from ANOVA on the effects of soil collection area (soil), conditioning species (species) and conditioning and their interactions on native biomass, conspecific biomass, RE$_H$ and RE$_C$**

	Native biomass			Conspecific biomass		
Factors	*F*	df	*P*	*F*	df	*P*
Soil	10.87	2	**<0.001**	124.43	2	**<0.001**
Species	6.08	3	**0.003**	38.23	3	**<0.001**
Soil * species	1.01	6	0.37	13.27	6	**<0.001**
Conditioning	1.14	1	0.29	0.09	1	0.76
Soil * conditioning	0.44	2	0.65	3.23	2	**0.04**
Species * conditioning	5.98	3	**<0.001**	16.78	3	**<0.001**
Soil * species * conditioning	0.83	6	0.55	6.19	6	**<0.001**
	RE$_H$			RE$_C$		
Soil	0.26	2	0.78	8.63	2	**<0.001**
Species	24.91	3	**<0.001**	37.21	3	**<0.001**
Soil * species	4.08	6	**0.003**	15.42	6	**<0.001**

RE is an index that examines the effect of PSF on the response generation while controlling for differences in soil fertility and resulting absolute plant size. Because conditioning is controlled for in the relative index (RE$_H$ and RE$_C$) so conditioning is not a factor included in that analysis. Significant *P* values are bolded.

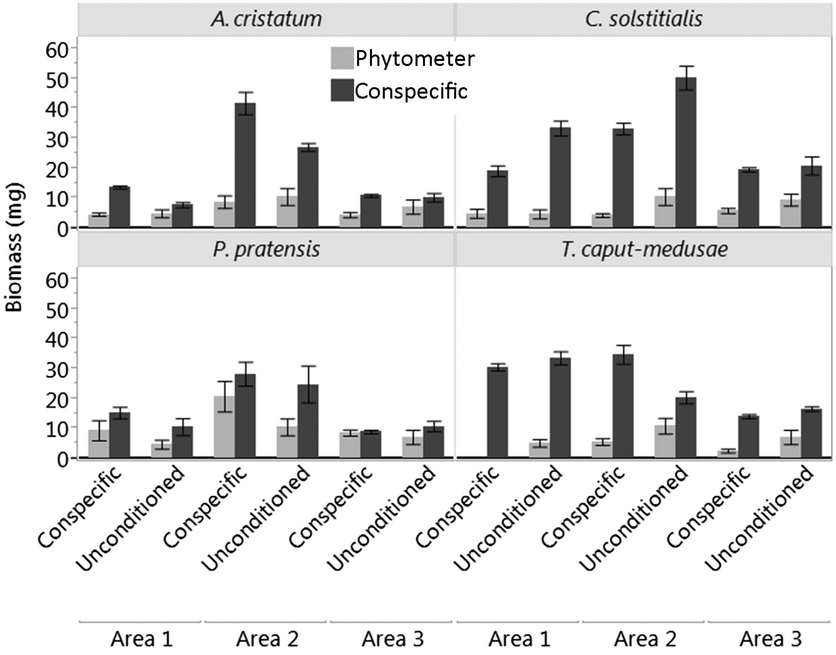

Figure 3: response generation biomass produced by invaders and the heterospecific native phytometer in unconditioned soil (previously unoccupied) and in soil conditioned by each invader in soils from three collection areas (Area 1, Area 2, Area 3). Each invader (*A. cristatum, C. solstitialis, P. pratensis* and *T. caput-medusae*) was only grown in unconditioned soil and conspecific conditioned soil (not soil conditioned by other invaders). Error bars indicate 1 SE.

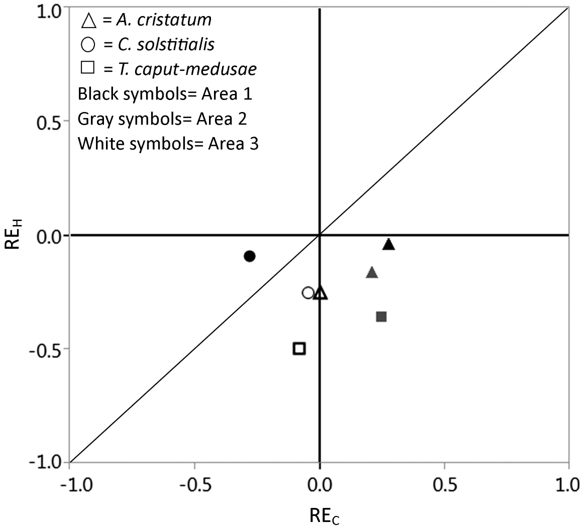

Figure 4: nonneutral PSFs plotted in RE value space (see Fig. 1).

on effects of other species in the community (Kulmatiski *et al.* 2011) and on initial abundance (Suding *et al.* 2013) and density (Levine *et al.* 2006) of invasive species.

Our results are consistent with accumulating evidence suggests that PSF may contribute to the invasive potential of *A. cristatum* (Jordan *et al.* 2008; Perkins *et al.* 2011; Perkins and Nowak 2013). Previous work that found *A. cristatum* produces a self-facilitatory feedback wherein conspecific plant biomass production was more than double in soil conditioned by *A. cristatum* compared to soil that was conditioned by native species (Jordan *et al.* 2008). Our results suggest that PSF does not uniformly contribute to the invasive potential of *C. solstitialis* or *P. pratensis*. Thus, PSF is likely unimportant in the invasion dynamics of these species. Cumulatively, this result combined with previous work suggest that the invasion of *C. solstitialis* is not consistently driven by PSFs and may be more related to species interactions and environmental conditions (Andonian *et al.* 2011; Andonian and Hierro 2011; Spencer *et al.* 2011; Young *et al.* 2011). Previous research has investigated allelopathy for a congener (*Centaurea stoebe* or *Centaurea maculosa*) of our study species (Aschehoug *et al.* 2014; Ridenour and Callaway 2001); however, no evidence of allelopathy has been found for *C. solstitialis* (Qin *et al.* 2007) and we did not investigate any aspects of allelopathy in our study. Our study is consistent with others (Jordan *et al.* 2012) who report that *P. pratensis* does not condition soils (specifically, alter soil fungi) differently than other invasive and native species.

Multi-site and multi-species studies, such as this one, have been proposed as one research direction that could overcome inadequacies of past research and improve predictive power and theoretical integration in invasion ecology (Kueffer *et al.* 2013). Although we did not examine PSF in soils collected from uninvaded and invaded areas for all four species and we only used one native phytometer, our study provides a technique for assessing the likelihood of further range expansion in any invasion where soil-mediated ecological interactions contribute to invasion. Many studies of invasive plant species focus on local-scale invasion dynamics due to the complexity

Table 3: mean RE values (SE), type of PSF generated by each species in each area and results from *t* tests

Invasive species	Area	RE_H	RE_C	Type of PSF
A. cristatum	**Area 1**	−0.04 (0.06)^{a}	0.28 (0.02)^{*b}	*Conspecific positive*
	Area 2	−0.16 (0.13)^{a}	0.21 (0.04)^{*b}	*Conspecific positive*
	Area 3	−0.25 (0.09)*	0.03 (0.02)	*Heterospecific negative*
C. solstitialis	**Area 1**	−0.09 (0.18)	−0.28 (0.04)*	Conspecific negative
	Area 2	−0.43 (0.06)*	−0.21 (0.03)*	Neutral
	Area 3	−0.25 (0.07)^{*a}	−0.03 (0.02)^{b}	*Heterospecific negative*
P. pratensis	Area 1	0.19 (0.20)	0.16 (0.06)	Neutral
	Area 2	0.22 (0.13)	0.04 (0.08)	Neutral
	Area 3	0.08 (0.06)	−0.10 (0.03)	Neutral
T. caput-medusae	**Area 1**	**	−0.05 (0.02)	*Heterospecific negative*
	Area 2	−0.36 (0.09)^{*a}	0.25 (0.04)^{*b}	*Conspecific positive*
	Area 3	−0.49 (0.10)^{*a}	−0.08 (0.03)^{b}	*Heterospecific negative*

Bold areas indicate that it is within the invasive species currently invaded range. RE_H and RE_C values within a row that are followed by different letters are significantly different from each other. Values indicated with a * are significantly different from zero. ** indicates that too few plants established for analysis. Invasive types of PSF are italicized.

of measuring ecological interactions at multiple field sites. There can be many ecological interactions that promote invasive species. Our study design allowed a unique opportunity to evaluate one specific process (PSF) in four invasive species and thus, to generate information that contributes to our larger knowledge base of the drivers of invasion (Kueffer *et al.* 2013). Our use of whole soil added ecological realism to our study of invasive potential in the greenhouse. We did not delve into the specific biotic or abiotic mechanisms that create the PSF (i.e. soil microbial community or soil nutrients).

Our results suggest that invasive PSFs are an ecological interaction that depends both on species identity and soil context. Only two of the four invasive species tested in this experiment consistently created invasive PSF types. This result is similar to results of other interactions or traits that contribute to invasive potential such as competitive ability (Vila and Weiner 2004), phenotypic plasticity (Palacio-López and Gianoli 2011) and dispersal ability (Flores-Moreno *et al.* 2013) to species invasion. Further, it is likely that these interactions or traits may interact with one another such as PSFs impacting competitive ability (Perkins and Nowak 2012) or PSF enabling a less competitive species to coexist with a highly competitive species (Zuppinger-Dingley *et al.* 2011). Combining process-based experiments with multiple species and a range of habitat types permits the examination of species and ecological dependence of interactions whose outcomes are the dominance of invasive species concomitant with native species suppression. Through these types of experiments, we may be able to begin to predict the dynamics and impacts of further range expansion in species that have already demonstrated invasive capacity.

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