Soil conditioning and plant–soil feedbacks affect competitive relationships between native and invasive grasses

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Abstract Understanding how competition from invasive species and soil conditions individually and interactively affect native performance will increase knowledge of invasion dynamics and can be used to improve the success of restoration plans. This study, conducted in Reno NV, USA, uses a two-phase plant–soil feedback experiment coupled with a target-neighbor competition design to examine the individual and interactive effects of both soil conditions and invasive neighbors on native performance. Study species include invasive species (*Bromus tectorum* and *Agropyron cristatum*) and native species (*Elymus elymoides* and *Pseudoroegneria spicata*). Results indicate that both plant performance and competitive interactions were influenced by species-specific soil conditioning. Specifically, invasive *B. tectorum* generated a larger competitive effect on natives than invasive *A. cristatum*; however, only *A. cristatum* conditioned soil in a manner that increased competitive effects of conspecifics on natives. Native *P. spicata* was relatively unaffected by soil conditioning and conversely, *E. elymoides* was strongly affected by soil conditioning.

Few previous studies have examined soil conditioning and the interaction of soil conditioning and neighbor effects that both are potentially important mechanisms in structuring plant communities and influencing plant invasion.

Introduction

Restoration of native plants into areas currently occupied by invasive plants is frequently attempted to control the negative impact of plant invasion on native species diversity (Grice 2009) albeit often with limited success (Eviner and Hawkes 2008; Jordan et al. 2008; Davies and Sheley 2011). Both above-ground effects (e.g., competition, Humphrey and Schupp 2004; Fansler and Mangold 2011) and belowground effects (e.g., plant–soil feedbacks, Jordan et al. 2008; Grman and Suding 2010) of invasive species limit the success of native species restoration. The competitive abilities of invasive species (Elton 1958; Vila and Weiner 2004; Blank 2010) and the impact of this competition during restoration is fairly well established (Eliason and Allen 1997; Cox and Allen 2011; Wainwright et al. 2012). However, the importance of plant–soil feedbacks on the success of native species restoration and on the competitive

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relationships between invaders and natives is less understood.

Plant–soil feedbacks (PSF) occur when plants alter soil conditions, such as soil biological community composition (Van der Putten et al. 1993) and soil nutrient availability (Dijkstra et al. 2006; Meisner et al. 2011; Perkins et al. 2011a) and thus influence subsequent plant performance (Bever 2003; Kulmatiski et al. 2008; Perkins and Nowak 2012). Research and meta-analysis indicate that, in general, most plants create PSFs that decrease subsequent conspecific performance (Kulmatiski et al. 2008). However, an increasing number of studies suggest that invasive species tend to either be unaffected by PSF or create PSFs that increase subsequent conspecific performance (van Grunsven et al. 2007; Perkins and Nowak 2012) and decrease subsequent heterospecific performance (Jordan et al. 2008). Previous research on how alteration of soil conditions affects competitive relationships is limited (Wardle et al. 2004; Bever et al. 2010; Kulmatiski et al. 2011). In addition, "aboveground implications of belowground processes" are not easy to predict (Wardle et al. 2004), may exert large effects on plant–plant interactions (Bever et al. 2010), and are needed to better understand invasion and restoration dynamics.

This study investigates (1) how performance of two native grass species is influenced by PSFs and by competition from invasive plants and (2) if PSF changes these competitive relationships. Specifically, this study questions how performance of natives *Elymus elymoides* and *Pseudoroegneria spicata* are affected by competing neighbors of invasive *Bromus tectorum* and *Agropyron cristatum* in soils previously occupied by either the native or the invaders (Fig. 1). Species were chosen so as to include two common native grasses and two common invasive grasses found within the Great Basin of the western US. Although *A. cristatum* has been intentionally seeded within the Great Basin during reclamation efforts, it meets the definition of an invasive species (non-native, able to expand populations over a considerable distance, and produce negative effects on native ecosystems, Richardson et al. 2000; Fansler and Mangold 2011). Our previous work on PSF dynamics of the study species (Perkins and Nowak 2012) indicates that both natives *E. elymoides* and *P. spicata* influence soil in a manner that benefits heterospecifics more than conspecifics. Invasive *A. cristatum* influences soil in a

manner that benefits conspecifics more than heterospecifics. Finally, invasive *B. tectorum* does not alter soil in a manner that significantly affects subsequent plant performance. These invasive species (*B. tectorum* and *A. cristatum*) do generate larger competitive effects than the native species in this study (*E. elymoides* and *P. spicata*), especially in seedling stages (Humphrey and Schupp 2004; Blank 2010; Gunnell et al. 2010). Competition from invasives has been observed to significantly decrease both *E. elymoides* and *P. spicata* seedling biomass in a glasshouse setting (Blank 2010; Gunnell et al. 2010) and in the field (Humphrey and Schupp 2004). Therefore, we hypothesized that natives would be negatively affected individually by invader presence and by conspecific PSF. We also hypothesized that the invader *A. cristatum* would have a larger competitive effect in soils previously occupied by conspecifics and that both invaders would have larger competitive effects on natives in soil previously occupied by the natives than in previously unoccupied soil. Because of limited knowledge regarding effects of soil conditions on competitive relationships, we generated our hypotheses on the straightforward reasoning that (1) if a plant has increased performance in conspecific-conditioned soil, it should also generate larger competitive effects on neighbors in that soil; and (2) if a species has decreased performance in conspecific-conditioned soil, it should also be more vulnerable to competition from neighbors in that soil.

Materials and methods

To examine effects of competition and plant–soil feedback on native species performance, a glasshouse experiment in two phases was conducted. During the soil conditioning phase, a first generation of plants were grown to condition (induce species-specific changes in) soil. The soil conditioning treatments include conditioning by each of the natives (*E. elymoides* and *P. spicata*), each of the neighbors (*B. tectorum* and *A. cristatum*), and an unconditioned control. For the unconditioned soil treatment, pots were filled with soil, but left unplanted and otherwise treated the same (e.g., received the same watering regime) as the planted pots. The second phase was the bioassay phase, wherein a target-neighbor design was established to determine competitive relationships in each of the soil conditioning
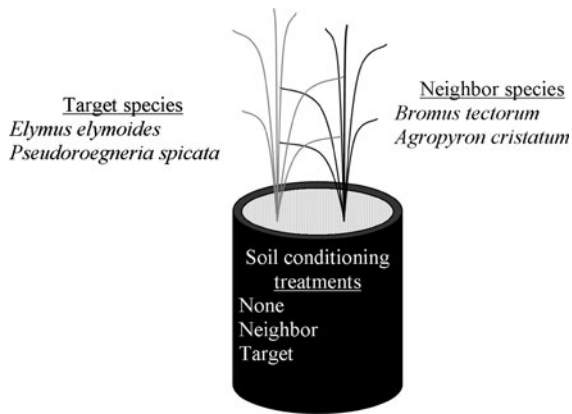
Fig. 1 Diagram of the experimental design. One individual plant of either target species (native grass species, *E. elymoides* and *P. spicata*) were grown with one individual of either neighbor species (invasive grass species, *B. tectorum* or *A. cristatum*), a conspecific, or with no neighbor in soil conditioned by either the target, the neighbor, or in unconditioned soil

treatments (Fig. 1). The experimental design for the bioassay phase included native species (*E. elymoides* and *P. spicata*) as targets growing in (1) unconditioned soil with either no neighbor, a conspecific neighbor, a *B. tectorum* neighbor, or an *A. cristatum* neighbor; (2) conspecific-conditioned soil with either no neighbor, a conspecific neighbor, a *B. tectorum* neighbor, or an *A. cristatum* neighbor; (3) *B. tectorum*-conditioned soil with either no neighbor, a conspecific neighbor, or a *B. tectorum* neighbor; and (4) *A. cristatum*-conditioned soil with either no neighbor, a conspecific neighbor, or an *A. cristatum* neighbor. Because the effect of the two invasive neighbors on each other was not of interest, the combination of *A. cristatum* as a neighbor in *B. tectorum*-conditioned soil and *B. tectorum* as a neighbor in *A. cristatum*-conditioned soil were not included (Fig. 1). The entire design was replicated 10 times.

Soil used for this project was native soil collected from Bedell Flats, a natural area approximately 40-km northeast of Reno, NV, USA. The soil is a Durinodic Xeric Haplargid (USDA, NRCS) and is a moderately fertile sandy loam (Perkins et al. 2011a). Major species in the area include sparse *Artemisia tridentata* and *Chrysothamnus nauseosus* although soil was collected from unvegetated areas. The top 20 cm of soil was collected, homogenized, and potted into RLC 3 containers (49 ml volume, Stuewe & Sons, Corvallis

OR USA) in a glasshouse in Reno, NV USA. The glasshouse was maintained to reflect typical growing season conditions, i.e., between 7 and 24 °C with ambient light. Distilled water was used to maintain pots near field capacity without allowing any leaching or overflow. Pots were randomly assigned to soil conditioning treatment and target-neighbor species, and pots were periodically rearranged to compensate for any environmental variation in the glasshouse.

In the first phase (the soil conditioning phase), several seeds were planted in each pot, but only the first emergent was allowed to grow. After 80 days of growth, aboveground biomass of the conditioning plants was removed. To transition to the second phase (target-neighbor bioassay phase), all soil conditioned by an individual species within one replicate was combined, homogenized, and then repotted. Seeds for the bioassay phase were planted within 1 day of the end of the soil conditioning phase. Several seeds of each target species and neighbor species were planted, and the first emergent of each species was allowed to grow. Date of emergence for each species within each pot was recorded. The growing season for the bioassay phase lasted for 80 days, after which all aboveground biomass was collected, dried at 60 °C for 24 h, and weighed.

A relative interaction index (R_{ii}, Armas et al. 2004) was adapted to calculate the net effect of soil conditioning (PSF response) and then the net balance of the interaction between plants grown alone and plants grown with neighbors within each soil conditioning treatment (Competition effect). The formulae for PSF response and for Competition effect are

$$PSF\,response = (B_c - B_a)/(B_c + B_a)$$

where B is the aboveground biomass of each species (growing without a neighbor) under each soil conditioning treatment (B_c) and the mean biomass of that species under other soil conditioning treatments (B_a) within each replicate.

$$Competition\,effect = (B_w - B_o)/(B_w + B_o)$$

where B is the aboveground biomass of a single plant growing with a neighbor (B_w) and alone (B_o). Competition effect was calculated separately for each soil conditioning treatment, i.e., the biomass of a target species growing with a neighbor in a given soil conditioning treatment and the biomass of a target

growing alone in that same soil conditioning treatment were used in the calculations.

A positive value indicates that a plant produced more biomass due to soil conditioning, or with a neighbor; a negative value indicates that a plant produced less biomass when grown in conditioned soil or without a neighbor.

Data were analyzed with PASW Statistics 18 (PASW for Windows, Rel. 18.0.0. 2009. Chicago: SPSS Inc.). Box-plots were used to examine for outliers, and Shapiro–Wilk was used to evaluate normality (no data were dropped and no transformations were necessary). Multivariate analysis was used to examine the effect of soil conditioning treatment, neighbor species, and the interaction of soil conditioning and neighbor species on target time to emergence, and examine biomass separately for each species. To minimize the potential for Type I error, MANOVA for overall effects and Tukey HSD comparisons for pairwise differences among soil conditioning treatments and neighbor species were used. In addition, separately for each species, univariate analyses (ANOVA) were conducted to examine the effect of soil conditioning treatment on PSF response and the effect of soil conditioning treatment, neighbor species, and the interaction of soil conditioning and neighbor species on competitive effect.

Results

Plant emergence was not affected by soil conditioning treatment or by neighbors (Table 1). Average time to *E. elymoides* emergence was 10.1 days (SE 0.2) and was not significantly affected by soil conditioning treatment, neighbor species ($p = 0.11$), or soil conditioning by neighbor interaction. Average time to *P. spicata* emergence was 8.7 days (SE 0.1) and was not significantly affected by soil conditioning species, neighbor species, or soil conditioning by neighbor interaction.

Soil conditioning had significant effects on both *E. elymoides* and *P. spicata* biomass (Table 1). The biomass produced by both *E. elymoides* and *P. spicata* was significantly different among soil conditioning treatments (Fig. 2). *E. elymoides* produced the most biomass in unconditioned soil, less biomass in *A. cristatum*- and *B. tectorum*-conditioned soils (22 and 35 % reduction, respectively), and the least

Table 1 Significance of soil conditioning treatment, neighbor species, and conditioning * neighbor interaction on target species *E. elymoides* and *P. spicata* emergence, biomass, competition, and PSF response

MANOVA	*E. elymoides*		*P. spicata*	
	$F_{(df)}$	p	$F_{(df)}$	p
Soil conditioning	**3.562**$_{(6)}$	**0.002**	**2.270**$_{(6)}$	**0.038**
Neighbor	**14.241**$_{(6)}$	**<0.001**	**22.216**$_{(6)}$	**<0.001**
Conditioning * neighbor	**4.428**$_{(14)}$	**<0.001**	1.213$_{(14)}$	0.267
Between-subject effects				
Emergence				
Soil conditioning	0.934$_{(3)}$	0.427	1.392$_{(3)}$	0.249
Neighbor	2.476$_{(3)}$	0.066	0.890$_{(3)}$	0.449
Conditioning * neighbor	1.757$_{(7)}$	0.104	1.182$_{(7)}$	0.318
Biomass				
Soil conditioning	**6.136**$_{(3)}$	**<0.001**	**3.678**$_{(3)}$	**0.014**
Neighbor	**29.550**$_{(3)}$	**<0.001**	**53.651**$_{(3)}$	**<0.001**
Conditioning * neighbor	**8.265**$_{(7)}$	**<0.001**	1.314$_{(7)}$	0.25
ANOVA				
Competition				
Soil conditioning	**20.437**$_{(3)}$	**<0.001**	0.546$_{(3)}$	0.652
Neighbor	**18.938**$_{(3)}$	**<0.001**	**58.295**$_{(3)}$	**<0.001**
Conditioning * neighbor	**5.052**$_{(7)}$	**<0.001**	0.656$_{(7)}$	0.709
PSF response				
Soil conditioning	**11.064**$_{(3)}$	**<0.001**	2.251$_{(3)}$	0.101

Values for emergence and target biomass were generated by MANOVA. Values for PSF response and competition were generated by separate ANOVAs. Significant values ($\alpha < 0.05$) are bold

biomass (57 % reduction) in its conspecific-conditioned soil. *Pseudoroegneria spicata* also produced the most biomass in unconditioned soil; however, the reduction of *P. spicata* biomass was only significant in conspecific-conditioned soil and *B. tectorum*-conditioned soil (32 and 26 % reduction respectively). Thus, the ability of both native species to produce biomass was significantly affected by soil conditioning treatments.

Neighbors had significant effects on both *E. elymoides* and *P. spicata* biomass (Table 1). The effects of neighbors on target performance was examined using biomass and competition effect values produced by each target species in the unconditioned soil (soil conditioning treatment "none" in Figs. 2, 4).
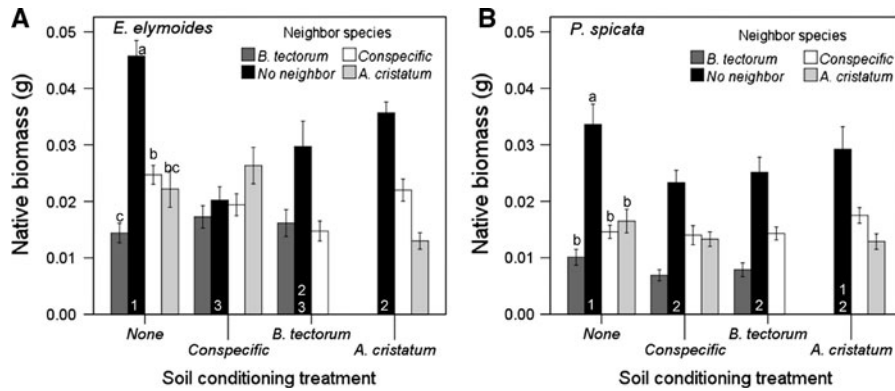
Fig. 2 Biomass produced by native grasses *E. elymoides* (**a**) and *P. spicata* (**b**) when grown alone and with neighbors in soils either previously unoccupied, or occupied by a conspecific or an invader (either *B. tectorum* or *A. cristatum*). *Bars* with *different letters* indicate a significant difference among neighbor species within one soil conditioning treatment. *Bars* with *different numbers* indicate a significant difference in the performance of the native grown with no neighbor among soil conditioning treatments. Significance was determined at a $p < 0.05$. *Error bars* are one SE

Patterns of competitive effects of neighbors on target biomass was common to both target species: (1) the presence of any neighbor significantly reduced target biomass; (2) the reduction in target biomass was not significantly different between conspecific and *A. cristatum* neighbors (46 and 52 % reduction of *E. elymoides* and 56 and 50 % reduction of *P. spicata* respectively); and (3) *B. tectorum* as a neighbor reduced target biomass the most (70 % reduction of *E. elymoides* and 71 % reduction of *P. spicata*). In general, *B. tectorum* produced larger competitive effects than *A. cristatum*.

Plant biomass in soils without neighboring species was used to test PSF response (Fig. 3). The stronger response of *E. elymoides* biomass production to soil conditioning treatments without neighbors resulted in a significant PSF response among soil conditioning treatments. *Elymus elymoides* experienced a significant negative PSF response in conspecific soil (Fig. 3). However, the response of *P. spicata* biomass production to soil conditioning treatments without neighbors was not enough to generate a significant PSF response (Fig. 3).

The interaction of soil conditions and neighbors were examined using competition effect values (Fig. 4). Neither native species was affected by neighbors more in their own conditioned soil than in the other soil conditioning treatments. Native *E. elymoides* was affected less by neighbors in its own conditioned soil than in unconditioned soil (represented by smaller competition effect values in
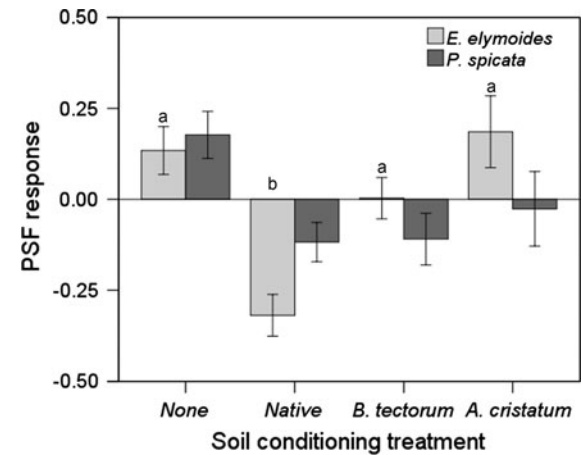
Fig. 3 Index showing the effect of soil conditioning (PSF) on native plant (*E. elymoides* and *P. spicata*) performance grown without neighbors. A positive value indicates that a plant produced more biomass in a given soil conditioning treatment than its mean biomass in all the treatments. *Bars* with *different letters* indicate a significant difference among soil conditioning treatments. Significance was determined at a $p < 0.05$. *Error bars* are one SE

the conspecific soil conditioning treatment than in other treatments, Fig. 2e), and native *P. spicata* tended to affected similarly by neighbors in its own conditioned soil compared to the unconditioned soil (Fig. 4). The effect of *B. tectorum* on *P. spicata* was consistently large and did not change among soil conditioning treatments (Fig. 4a). However, for *E. elymoides*, the competitive effect of *B. tectorum* was significantly different among soil conditioning treatments. *Bromus tectorum* produced the largest competitive effect in the

Fig. 4 Index showing the effect of neighbors on native plant performance among the soil conditioning treatments. A negative value indicates that native plant biomass was reduced by neighbor's presence. *Bars* with *different letters* indicate a significant difference among soil conditioning treatments. Significance was determined at a $p < 0.05$. *Error bars* are one SE
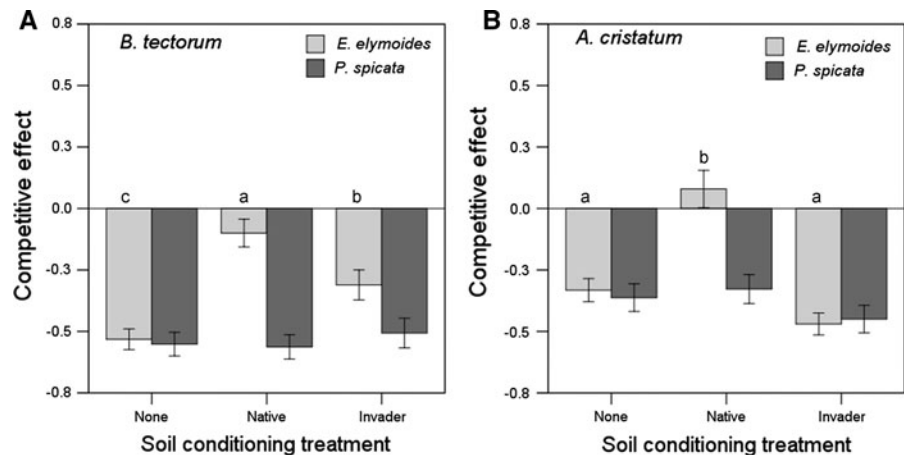
unconditioned soil and the least in *E. elymoides* conspecific-conditioned soil (Fig. 4a). The competitive effect of *A. cristatum* on native *E. elymoides* (Fig. 4b) was significantly larger in *A. cristatum*-conditioned soil than in *E. elymoides* conspecific-conditioned soil. The competitive effect of *A. cristatum* on native *P. spicata* was not different among soil conditioning treatments (Fig. 2b).

Discussion

Performance of native species was affected by both aboveground (competition) and belowground (PSF) effects of invaders. More importantly, PSF changed competitive relationships between natives and invaders. This evidence that soil conditioning can influence competitive relationships has implications both for understanding plant population dynamics, plant community interactions, invasion dynamics, and ecological restoration (Wardle et al. 2004; Bever et al. 2010; van de Voorde et al. 2011). The effect of soil conditioning on competitive relationships can influence invasion dynamics as either an ability of the invader or as a characteristic of the potentially invaded system (Perkins et al. 2011b). The ability of some species, such as *A. cristatum*, to create PSFs that increase conspecific performance and competitive ability may increase their invasive potential (Klironomos 2002; Kulmatiski et al. 2008). Further, sites occupied by natives, such as *E. elymoides*, that condition soils in a manner that decreases subsequent conspecific performance or increase heterospecific performance (e.g., *P. spicata*, Perkins and Nowak 2012) might be especially

vulnerable to invasion. Restoration of sites occupied by invaders that benefit from their own soil conditioning (e.g., *A. cristatum*) may require more attention to belowground conditions (Grman and Suding 2010) than sites occupied by invaders that do not benefit from soil conditioning (e.g., *B. tectorum*).

Interestingly, the invaders showed two different interactive relationships between competitive ability and plant–soil feedbacks. Invader *B. tectorum* had consistently high competitive ability in all but one of the soil conditioning treatments (Figs. 2, 4). *Bromus tectorum* did not produce significant PSFs (Fig. 3) and its competitive ability did not change substantially among most soil conditioning treatments. Conversely, invader *A. cristatum* only produced higher competitive effects than the native's conspecific neighbors in its conspecific-conditioned soil (Figs. 2, 4). Thus, the invasive potential (Perkins et al. 2011b) of *B. tectorum* may be derived from competitive ability and not soil conditioning and the invasive potential of *A. cristatum* may be derived from soil conditioning more than competitive ability. Like *A. cristatum*, other invasive plants are also thought to be successful invaders due to the changes they create in their soil environment more than their competitive ability. For example, *Typha × glauca* invasion in coastal marshes has been attributed to its ability to alter soil conditions in a manner that decreases heterospecific performance and increases conspecific performance more than its competitive ability (Farrer and Goldberg 2009).

The plant–soil feedback generated by invader *A. cristatum* is worthy of note. Soil conditioned by *A. cristatum* resulted in increased *E. elymoides* performance indicated by a positive PSF response

value (Fig. 3). This result is consistent with previous work that indicates that *A. cristatum* may produce plant–soil feedbacks that increase subsequent plant growth (Jordan et al. 2008; Perkins and Nowak 2012). However, this benefit to heterospecifics may only manifest when they are growing alone. *Agropyron cristatum* has been observed to produce a conspecific-positive feedback type, meaning all subsequent plant growth is promoted, but conspecifics have a larger response than heterospecifics (Perkins and Nowak 2012). Although soil conditioned by *A. cristatum* might benefit *E. elymoides* growing alone, the benefit to subsequent *A. cristatum* performance (increased biomass production, Perkins and Nowak 2012) and competitive ability (Fig. 4) outweigh any benefit to a native growing alongside the invader.

These results have several implications for restoration and provide an example that "one way fits all" restoration plans are not sufficient (Kardol and Wardle 2010). Native *E. elymoides* performed especially poorly in conspecific-conditioned soil; therefore, seeding *E. elymoides* into soils that previously had *E. elymoides* present might be less successful than into other soils. Native *P. spicata* was impacted by neighbor presence, but not by PSF; therefore, restoration of *P. spicata* should focus on neighbor presence more than soil conditioning. Based on the result that invader *B. tectorum* induced a large competitive effect on native performance but did not have more of an effect in its own conspecific-conditioned soil, a restoration plan involving *B. tectorum* may need to address the invader's presence more than soil conditions. Conversely, invader *A. cristatum* did not produced competitive effects that were significantly different from the competitive effect produced by the native's conspecific neighbor except in its own conditioned soil; therefore, a restoration plan involving *A. cristatum* may need to address soil conditions as well as invader presence. Restoration strategies that address soil conditioning may include planting native species that are less affected by soil conditioning (van de Voorde et al. 2011) or amending the soil to remove the conditioning effects (Grman and Suding 2010). Also, reclamation plans that involve intentionally introducing *A. cristatum* for site stabilization should be cautiously considered as native species at these sites may be negatively impacted by soil conditioning.

How alteration of soil conditions affects competitive relationships in a natural setting may only marginally be anticipated by a target-neighbor competition in soils conditioned for one generation in a glasshouse setting. Studies on PSFs in a glasshouse usually find stronger effects than field studies (Kulmatiski et al. 2008), and PSFs may change with increasing plant density and neighbor identity (Blank 2010). Therefore, this project can be used to generate hypotheses (Freckleton and Watkinson 2000) for further testing. Appropriate hypotheses might address how soil conditioning changes with increasing conspecific and heterospecific neighbors, how PSFs compound and change over time, and how PSFs manifest under field (compared to controlled glasshouse) temperature and water availability conditions. This study only examined the target-neighbor relationship for 80 days (emergence and seedling life stages) and relationships that reduce target performance at the seedling stage may change to neutral or positive at later life stages (Leger and Espeland 2010; Farrer and Goldberg 2011). However, our results agree with other target-neighbor competition studies that include these species (Blank 2010; Gunnell et al. 2010). Blank (2010) also found *P. spicata* was more negatively affected by *B. tectorum* neighbors than conspecific neighbors, and Gunnell et al. (2010) also found *E. elymoides* and *A. cristatum* induce similar competitive effects. The negative effect of *B. tectorum* on *E. elymoides* has been observed to continue through 2 years in the field (Humphrey and Schupp 2004).

In summary, this project provides evidence that prior vegetation has potential to influence subsequent native plant performance and competitive relationships with neighbors. Specifically, both natives were negatively impacted by the presence of neighbors, and for *E. elymoides*, these competitive relationships changed with soil conditioning treatments. Invader *A. cristatum* generated a PSF that increased its competitive ability and *B. tectorum* created a consistently large competitive in most soil conditioning treatments.

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