

Live long and prosper: plant–soil feedback, lifespan, and landscape abundance covary

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Abstract. Plant soil feedbacks (PSFs) are thought to be important to plant growth and species coexistence, but most support for these hypotheses is derived from short-term greenhouse experiments. Here we use a seven-year, common garden experiment to measure PSFs for seven native and six nonnative species common to the western United States. We use these long-term, field-based estimates to test correlations between PSF and plant landscape abundance, species origin, functional type, and lifespan. To assess potential PSF mechanisms, we also measured soil microbial community composition, root biomass, nitrogen cycling, bulk density, penetration resistance, and shear strength. Plant abundance on the landscape and plant lifespan were positively correlated with PSFs, though this effect was due to the relationships for native plants. PSFs were correlated with indices of soil microbial community composition. Soil nutrient and physical traits and root biomass differed among species but were not correlated with PSF. While results must be taken with caution because only 13 species were examined, these species represent most of the dominant plant species in the system. Results suggest that native plant abundance is associated with the ability of long-lived plants to create positive plant–soil microbe interactions, while short-lived nonnative plants maintain dominance by avoiding soil-borne antagonists, increasing nitrogen cycling and dedicating resources to aboveground growth and reproduction rather than to belowground growth. Broadly, results suggest that PSFs are correlated with a suite of traits that determine plant abundance.

Key words: *common garden; exotic; field experiment; nonnative species; nutrient plant–soil feedback; physical plant–soil feedback; semiarid; shrub–steppe; soil DNA.*

INTRODUCTION

Plant–soil feedbacks (PSFs) have gained attention as an explanation of plant growth and coexistence (van der Heijden et al. 2008, van Der Putten et al. 2013, Bailey and Schweitzer 2016). PSFs are typically measured by comparing plant growth on soils cultivated by conspecifics (i.e., self-cultivated or “self”) to plant growth on soils cultivated by heterospecifics (i.e., other-cultivated or “other”; Bever 1994, Kulmatiski and Kardol 2008, Reinhart and Rinella 2016). Plants that grow better on self soils have positive PSFs, while plants that grow better on other soils have negative PSF (Bever 1994). Mathematical models suggest that negative PSFs encourage species coexistence through species replacements, though this assumes feedback effects are stronger than competition effects (Bever et al. 1997, Kulmatiski et al. 2016, Vincenot et al. 2017). Because plants are rarely competitively equivalent and observing species replacements requires multi-generation experiments, explicit tests of

model predictions remain uncommon (van Der Putten et al. 2013, Kulmatiski et al. 2016). Instead, some of the best support for the role of PSFs comes from correlations between PSF and plant abundance on the landscape, though these tests also remain uncommon (Klironomos 2002, Mangan et al. 2010, Bennett et al. 2017).

Although the number of experiments measuring PSF has increased rapidly in the past 10 years, most studies remain limited to short-term (i.e., ~6 month) greenhouse conditions (Kulmatiski et al. 2008, Bennett and Cahill 2016, Heinze et al. 2016, Schittko et al. 2016). The need for a better understanding of longer-term PSF under field conditions has been identified as a primary goal for understanding the role of PSFs in species growth and coexistence (Harrison and Bardgett 2010, van Der Putten et al. 2013, van der Putten et al. 2016).

There are many reasons that PSF may differ between greenhouse and field conditions and we highlight a few here (Ehrenfeld et al. 2005, Schittko et al. 2016, van der Putten et al. 2016). Greenhouse experiments typically inoculate sterilized growth media with soils cultivated by target plant species. This approach is likely to encourage the growth of fast-growing or fast-moving microbial species and their predators (Poorter et al. 2016). Under field conditions, it is likely to be more difficult for plants

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to change the composition of soil microbial communities that are more abundant and diverse than those in the greenhouse (Kulmatiski and Beard 2011, Hawkes et al. 2013, Kardol et al. 2013). Similarly, greenhouse experiments are typically performed in warm, wet conditions that favor some soil organisms or plants over others (Poorter et al. 2016). Under field conditions, variable and extreme climate conditions are likely to create different plant–soil interactions (van der Putten et al. 2016, Smith-Ramesh and Reynolds 2017). Additionally, greenhouse experiments often use nutrient additions or small-volume soil inoculations to control for potential differences in nutrient cycling caused by different plant species (i.e., plant–nutrient feedbacks; Ehrenfeld et al. 2005). Field experiments are less likely to use this approach and therefore measure both plant–microbe and plant–nutrient feedbacks. Finally, in small pots that are often moved in the greenhouse, plants are less likely to develop physical soil conditions that can feedback to affect subsequent plant growth (i.e., plant–physical soil feedbacks; Kyle 2005, Kyle et al. 2007, Bergmann et al. 2016).

In addition to measuring and testing the importance of PSF in field conditions, a second major goal of PSF research over the past several years has been to identify patterns in PSF associated with plant traits (Baxendale et al. 2014, Ke et al. 2015, Fitzpatrick et al. 2016, Deyn 2017, Sweet and Burns 2017). For example, PSFs are thought to become less negative for later-successional species (Kardol et al. 2006). Similarly, studies have suggested that PSFs are more negative for grasses than forbs and for native than nonnative plants (van Grunven et al. 2007, Kulmatiski et al. 2008). Despite these examples, there remains a recognized need for tests of how plant abundance, plant types and plant traits are associated with PSFs (van Der Putten et al. 2013, van der Putten et al. 2016).

Our overarching objective was to measure the direction, strength, and potential mechanisms of PSFs in a common-garden field experiment for some of the dominant native and nonnative plant species in a shrub–steppe ecosystem. More specifically, we measured PSFs for seven common native and six common nonnative species using a four-year conditioning phase (Phase 1) and a three-year test phase (Phase 2) in a common-garden field experiment, Winthrop, Washington, USA. PSF was measured using a “self vs. other” approach in which plant growth on self-cultivated soils was compared to plant growth on vegetation-free, “control” soils. As a test of whether or not these PSFs were important to plant growth in natural communities, we compared PSF values to plant abundance on the landscape (Klironomos 2002, Mangan et al. 2010, Maron et al. 2016). To test for general patterns in PSF among different plant types, we compared PSF values among native and nonnative plants, grasses, and forbs, and short- and long-lived plants. In an attempt to identify potential mechanisms of PSF, we describe the soil microbial communities, root biomass, soil nitrogen cycling, and soil physical properties associated with each

plant species and correlate results with PSF and plant abundance on the landscape.

METHODS

Research was conducted in a field on the Newbon soil series (coarse-loamy, mixed mesic Typic Haploxerolls; Lenfesty 1980) near the Washington Department of Fish and Wildlife, Methow Wildlife Area headquarters, Winthrop, Washington (48.481° N, 120.117° W; elevation 780 m). The biotic and abiotic conditions of the valley have been described elsewhere (Kyle 2005, Kulmatiski 2006, Kulmatiski et al. 2006, Warren et al. 2015). Briefly, mean annual precipitation between 1971 and 2000 was 380 mm. There are two common plant community types in the surrounding landscape: fields that have never been tilled represent most of the land and are dominated by native plants and fields that have been tilled and abandoned from agricultural use are dominated by nonnative plants (Kulmatiski 2006). A vegetation survey of 25 paired fields revealed that native plants covered $43\% \pm 2\%$ of the ground (mean \pm SD) in never-tilled fields and $4\% \pm 1\%$ of the ground in abandoned-agricultural fields (Kulmatiski 2006). In contrast, nonnative plants covered $38\% \pm 3\%$ of the ground in abandoned-agricultural fields and $4\% \pm 1\%$ of the ground in never-tilled fields (Kulmatiski 2006).

Plant–soil feedback experiment

A roughly 1-ha area in a field that was abandoned from alfalfa (*Medicago sativa*) production several years prior to this research was used to establish a two-phase PSF experiment (Bever 1994, Kulmatiski and Kardol 2008). Prior to Phase 1, the top 10 cm of soil was removed by bulldozer to remove the weed seed bank. As is common for the Newbon soil series, this removed the A1 soil layer but the 25 cm thick A2 layer remained (Lenfesty 1980). Soils (7.6 m³) from a nearby native-dominated field were mixed with equal amounts of sand from a nearby landslide to add roughly 6 cm of native soil inoculum. Native soil was collected from a field where the ground cover of dominant plants was 31% *Purshia tridentata*, 22% *P. spicata*, 19% *B. sagitata*, 4% *Artemisia tridentata*, 4% *L. sericeus*, 2% *Lithospermum arvensis*, and 2% *B. tectorum* (A. Kulmatiski, *personal observation*). Species naming follows that of Hitchcock and Cronquist (1973). Several passes with a disc plow were used to mix the agricultural, native, and sand soils in the top 15 cm.

A grid of 1.2 m-wide geotextile cloth was secured to the ground creating 1,170 1.5-m² plots. Each of the 13 target species was planted in 65 randomly selected replicate quadrats. The remaining 325 unplanted plots were used to make 25 replicate control plots in Phase 2 for each species. Plant cover in these control plots was used as other growth in PSF calculations. Each fall from 2006 to 2009, 12 g of seed from the target species was added to

each self plot; a rate suggested to saturate germination space (Sheley et al. 1997). Each spring and summer from 2007 to 2010, non-target species were removed from each plot by hand weeding. During Phase I, control plots typically contained naturally recruiting plants, but were weeded several times each season. These soils were intended to be analogous to interspace soils and produce soils that were more similar to other soils than to sterilized soils commonly used in greenhouse experiments.

Dominant species from native and nonnative communities on the landscape were selected for this experiment with some exceptions (Table 1). Because the experiment was conducted in 1.5-m² experimental plots, the large native shrubs *P. tridentata* and *A. tridentata* were not used. The native annual forb *Collomia grandiflora* is not a dominant species but it is common and was used to gain inference from a native annual. Among nonnatives, *Cardaria draba* is a dominant species, but it was not used because the growth of this rhizomatous plant was unlikely to be contained within 1.5-m² experimental plots. *Poa bulbosa* is also dominant but was not used because we were unable to grow it under greenhouse or field conditions. The seven native species represented 70% of total and 87% of herbaceous plant cover in native plant communities (Kulmatiski 2006). The six nonnative species represented 28% of the total cover in nonnative plant communities, but 45% of the nonnative weedy species (i.e., not agricultural or native species). Lifespans for these species were estimated from the literature (Table 1; Appendix S1).

In May 2010, percent cover by species was determined by visual estimation in all plots. Plots where the target species did not represent 65% or more of standing vegetation were removed from the experiment. This resulted in 9–65 plots for each species with a mean of 35 plots per

species (Appendix S1: Table S1). Beginning June 2010, all remaining control and self quadrats were treated with a broad-spectrum herbicide application (30 mL of Roundup herbicide [Monsanto, St. Louis, Missouri, USA], 0.2 kg active ingredient/ha). Two weeks later, standing vegetation was clipped by hand and left in the plot. Plots were revisited over the next several months and additional herbicide spot-treatments and hand-pulling were used in quadrats where regrowth was observed.

In October 2010, we started Phase 2 of the experiment. Each species was replanted by seed as monocultures in self and control plots. Bare control plots were used as other soils. Non-target species were removed from all plots during the 2011, 2012, and 2013 growing seasons. Percent cover of each plant was measured in each plot using visual estimation in the 2011 and 2013 seasons, but only data from the end of the experiment, June 2013, are reported.

Microbial analyses

To characterize microbial communities associated with each target species, at the end of Phase 1, May 2010, soil cores (4 cm width by 15 cm depth) were collected from the center of eight randomly selected, target-species plots. Cores were returned to the laboratory and frozen (–40°C) until DNA extraction. Soil was thawed, passed through a 2-mm sieve, moisture content determined, and 0.25 g subsample taken. DNA was extracted (Power soil extraction kit; MoBio Laboratories, Carlsbad, California, USA), quantified and quality checked by spectroscopy (Nanodrop, Wilmington, Delaware, USA). Bacterial 16S ribosomal V4-V5 hypervariable region (He et al. 2010) and the fungal ITS2 region (Martin and Rygielwicz 2005) were amplified for sequencing. Pyrosequencing of PCR

TABLE 1. Classifications for species used in the plant–soil feedback experiment.

Species	Code	Growth form	Landscape abundance† (%)	Lifespan‡ (yr)	Variety	Source
Natives						
<i>Balsamorhizae sagittata</i>	BASA	Forb	15.3	40	unknown	Rainier
<i>Collomia grandiflora</i>	COGR	Forb	0.4	0.4	unknown	Milestone Nursery
<i>Festuca idahoensis</i>	FEID	Grass	2.9	19	Joseph	Rainier
<i>Koeleria cristata</i>	KOCR	Grass	0.2	8	Zumwalt	BFI
<i>Lomatium dissectum</i>	LODI	Forb	1.2	8	local	Friends of the trees
<i>Lupinus sericeus</i>	LUSE	Forb	4.3	15	unknown	Granite seed
<i>Pseudoroegneria spicata</i>	PSSP	Grass	18.9	46	Duffy Creek	BFI
Nonnatives						
<i>Agropyron cristatum</i>	AGCR	Grass	1.5	27	P27	Rainier seed
<i>Bromus tectorum</i>	BRTE	Grass	4.5	0.3	local	hand-collected
<i>Centaurea diffusa</i>	CEDI	Forb	5.1	1.5	local	hand-collected
<i>Lactuca serriola</i>	LASE	Forb	1.0	0.5	local	hand-collected
<i>Sisymbrium loeselii</i>	SILO	Forb	3.0	1.5	local	hand-collected
<i>Tragopogon dubius</i>	TRDU	Forb	1.7	0.6	local	hand-collected

†Landscape abundances extracted from Kulmatiski (*unpublished manuscript*) and represent the average percent cover of each species in 25 fields.

‡Literature sources for lifespan estimates provided in Appendix S1.

amplicons was performed with the 454 FLX Systems (454 Life Sciences, Branford, Connecticut, USA) with a sample tagging approach using 8 bp barcodes on the forward fusion primer. The PCR reaction mixture contained $1 \times$ PCR buffer (MgCl_2 plus), 0.2 mmol/L dNTPs, 0.2 $\mu\text{mol/L}$ of each forward and reverse primers, 0.05 U of enzyme (FastStart High Fidelity Enzymes Blend; Roche Life Sciences, Branford, Connecticut, USA), and 1.0 μL of template DNA in a 50 μL reaction. Amplification was as specified by the primer sets 515F and 907R and 5.8A1 and ITS4 for bacteria and fungi, respectively. The PCR products were checked by agarose gel electrophoresis, and cleaned by Agencourt AMPure XP (Beckman Coulter, Brea, California, USA). The DNA concentration of the purified PCR product was measured using the Quant-iT PicoGreen dsDNA BR Assay Kit (Invitrogen, Carlsbad, California, USA) then 36 products were pooled in equal molar concentration into a set. Each set was sequenced unidirectionally from the forward primer on a GS FLX+XLR70 Instrument using the GS FLX Titanium emPCR Kit (Lib-L) in one region of the plate (eight regions per plate).

Root biomass and soil nitrogen and physical traits

To characterize soil physical characteristics associated with each target species, soil cores were taken from the center of 16 randomly selected self plots during peak growing season at the beginning of Phase 2, June 2011. Soils were dried to constant mass at 70°C, passed through a 2-mm sieve, and all roots were separated and weighed and reported as grams of root biomass per kg soil. These same soil cores were used to estimate soil bulk density.

At the same time as soil core sampling, soil penetration resistance and shear strength were measured in 16 self plots for each species. Within each plot, three subsample measurements were taken at three fixed locations in each plot. Sub-sample measurements were averaged prior to analyses. Measurements (kg/cm^2) were made with handheld penetrometer (Certified Materials Testing Products, Palm Bay, Florida, USA) and a Torvane shear device (Durham Geo Slope Indicator, Stone Mountain, Georgia, USA).

To estimate net-N mineralization, two soil cores were taken from eight randomly selected self plots from each plant species (Robertson et al. 1999). One soil core was taken for immediate extraction of inorganic N (i.e., T_0), and the second was placed in an unsealed plastic bag and returned to the soil core hole for a one-month incubation (i.e., T_1). Inorganic N was extracted from a roughly 10-g subsample soil (<2 mm) using a 10:1 soil to 2 mol/L KCl ratio by mass. Extractants were analyzed for ammonium (NH_4^+) and nitrate (NO_3^-) concentrations on a Lachat Quickchem 8000 Flow Injection Analyzer (Lachat Instruments, Loveland, Colorado, USA). Net-N mineralization was calculated as the difference in the sum of extractable ammonium and nitrate between the two sample dates (i.e., $T_1 - T_0$; Robertson et al. 1999).

Note that soil microbial, chemical, and physical samples were not collected from *L. dissectum* plots due to early plant senescence and sampler error.

Statistical analyses

We used plant cover at the end of Phase 2 primarily to calculate PSF (see next paragraph), but we also tested PSF for differences in plant cover among species using a one-way generalized linear mixed model (Proc Glimmix in SAS v 9.4; SAS Institute, Cary, North Carolina, USA; Brinkman et al. 2010).

PSF was calculated as $(S - O)/\max(S, O)$ where S is the percent cover of the target species on self-cultivated soils and O is the percent cover of the target species on other soils (i.e., control soils in this study; Kulmatiski and Kardol 2008, Brinkman et al. 2010). A bootstrapping approach was used to estimate PSF values and the variation associated with the PSF values (Carvalho et al. 2010, Schittko et al. 2016). A random bootstrap sample of the plant cover on self soils and a second random bootstrap sample for plant cover on control soils were taken and used to calculate the feedback value and repeated 200 times by sampling with replacement. The resulting bootstrapped sample was used to construct 95% bootstrap confidence intervals to determine if PSF values were different from each other or zero. Values with non-overlapping confidence intervals are assumed significantly different. To test whether PSFs were different for categorical plant traits (i.e., native vs. nonnative and forbs vs. grasses), t tests were used and species PSF was the unit of replication.

We used correlations to determine if PSF was associated with plant abundance on the landscape. Landscape abundance was determined for native and nonnative plants separately because these plants create distinct communities on the landscape (Kulmatiski 2006). As a result, correlations with plant abundance represent the relationship between PSF and native plant abundance in native plant communities and nonnative plant abundance in nonnative communities. We similarly used correlations to test for a relationship between PSF and plant lifespan. To help identify PSF mechanisms, we tested whether plant species influence each of the following using a completely randomized, one-way generalized linear model where plant species was the factor: soil penetration resistance, soil shear strength, soil bulk density, net-N mineralization, and root biomass. To test whether or not these traits were associated with PSF or landscape abundance, correlations were used. All analyses were performed in SAS v 9.4 using Proc Glimmix, Proc Reg, and Proc ttest.

Microbial communities.—Amplicon sequences were analyzed using QIIME pipeline (Caporaso et al. 2010). The raw counts of archaeal, bacterial, and fungal operational taxonomic units (OTUs; defined as 97% gene sequence similarity) were transformed into proportion values and analyzed by nonmetric multidimensional scaling (NMS). NMS was performed using Bray-Curtis distance

matrices using meta-NMS in the vegan package in the R programming language (R Core Development Team 2004). To test for species effects on soil microbial community composition, we performed permutation multivariate analysis of variance (PERMANOVA) using the adonis command (Oksanen et al. 2007). To identify NMS axes that best described differences among plant species, the envfit command was used. The two axes that best separated microbial communities as a function of the plants that cultivated those communities were compared further to PSF values and landscape abundance using linear regression in SAS using Proc Reg. Finally, to identify OTUs that were most likely to cause observed microbial community effects on plant growth the ‘envfit’ command was used to identify OTUs that were best correlated with selected NMS axes.

RESULTS

On self soils, species differed in the ground cover they attained ($F_{12,449} = 10.03$, $P < 0.0001$; Appendix S1: Table S1). *B. sagittata*, *C. diffusa*, and *P. spicata*, the three dominant species on the landscape, produced the most ground cover. Species also differed in ground cover on control soils ($F_{12,221} = 13.91$, $P < 0.0001$; Appendix S1: Table S1). On control soils, *K. cristata* and *C. diffusa* produced the most ground cover.

These growth responses resulted in both positive and negative PSFs for both native and nonnative species (Fig. 1). Among natives, the dominant species on the landscape, *P. spicata* and *B. sagittata* demonstrated the most positive PSFs, while the less common forb *L. dissectum* and the annual forb *C. grandiflora* demonstrated negative PSFs. Among nonnatives, *L. serriola*, *B. tectorum*, and *A. cristatum* demonstrated positive PSFs, and only the

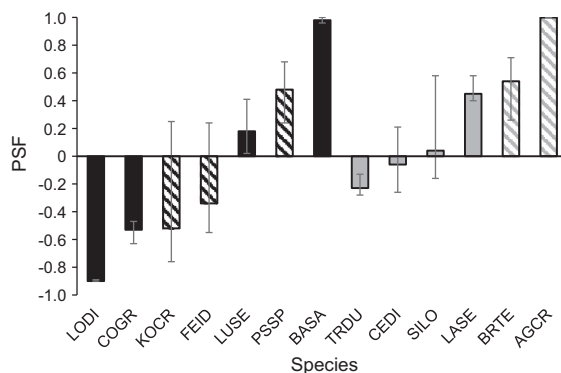


FIG. 1. Plant–soil feedbacks (PSF) for seven dominant native (black) and six dominant nonnative (gray) plant species, Winthrop, Washington, USA. PSFs measured after a four-year conditioning phase and three-year test phase in a common garden experiment. Values represent bootstrapped means and 95% confidence intervals. Confidence intervals that do not overlap zero indicate significantly positive or negative values. Confidence intervals that do not overlap between species indicate differences between species. Solid colors indicate forbs and hatched colors indicate grasses. Species codes defined in Table 1.

annual forb *T. dubius* demonstrated a negative PSF. There were no differences between PSF values for native vs. nonnative ($T_{1,11} = 1.41$, $P = 0.26$), grass vs. forb ($T_{1,11} = 0.49$, $P = 0.50$) or annual vs. perennial ($T_{1,11} = 0.07$, $P = 0.80$).

There was a positive correlation between PSF and plant abundance on the landscape for natives ($F_{1,6} = 12.92$, $P = 0.02$, $R^2 = 0.75$) but not for nonnatives ($F_{1,5} = 1.11$, $P = 0.35$; Fig. 2).

There was a positive correlation between PSF and plant lifespan for natives ($F_{1,6} = 12.03$, $P = 0.02$, $R^2 = 0.73$), but not for nonnatives (Fig. 3; $F_{1,5} = 4.03$, $P = 0.12$).

Because PSF was correlated with landscape abundance, we tested for relationships between potential PSF mechanisms (i.e., plant–microbial, plant–nutrient, and plant–physical feedbacks) and PSF and landscape abundance to identify potential explanations of observed PSF. NMS analyses revealed a “plate” effect in which sample sequences were longer on one sample plate than another. Because we not interested in this plate effect, we did not examine NMS axes for which plate effects were significant. As a result, NMS axes 3 and 5 were analyzed (envfit $R^2 = 0.29$, $P = 0.05$ for plant species effects). Soil microbial communities differed among species (Fig. 4; $F_{1,11} = 2.19$, $P = 0.001$, $R^2 = 0.38$). NMS axis 5 values were correlated with PSF values (Fig. 5a; $F_{1,11} = 8.29$, $P = 0.016$, $R^2 = 0.45$) and plant landscape abundance (Fig. 4b; $F_{1,11} = 5.28$, $P = 0.044$, $R^2 = 0.28$). Among bacteria and archaea, the following five bacterial OTUs (phylum, class, order) were best correlated with NMS 5 values: Planctomycetes Phycisphaerae Cpla-3; Gemmatimonetes, Gemmatimonetes Kd8-87, Verrucomicrobia unknown unknown, Bacteroidetes Saprospirae unknown and Bacteroidetes Saprospirae Saprospirales (Appendix S1: Table S2). No significant correlations were found with NMS 3. Among fungi, the following five OTUs (phylum, class, order) were best correlated with NMS 5 values: Basidiomycota Tremellomycetes Filobasidiales,

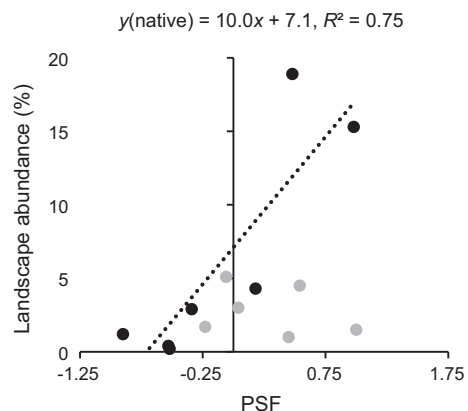


FIG. 2. Landscape abundance (%) vs. plant–soil feedback (PSF) for the seven native plants (native) and for the six nonnative plants. Data for native plants in black. Data for nonnative plants in gray. The correlation was significant for native but not for nonnative plants.

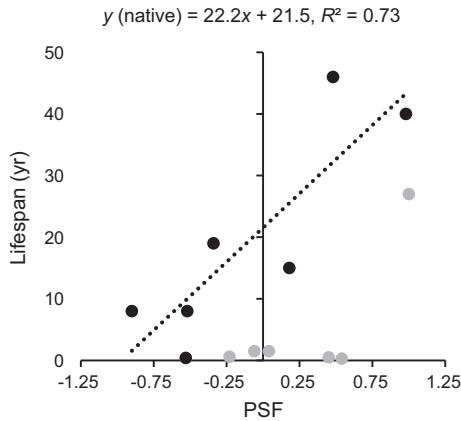


FIG. 3. Nonmetric multidimensional scaling (NMS) ordination graph of the soil microbial community found in soils in a common garden experiment cultivated by different plant species for four years. The microbial community was defined by the genetic sequences for archaeal, bacterial, and fungal organisms. Black and gray symbols represent soils cultivated by native and nonnative plant species, respectively. Solid and hatched symbols represent forbs and grasses, respectively. See Table 1 for species codes.

Ascomycota Sordariomycetes unknown, Ascomycota Dothideomycetes Pleosporales, Ascomycota Dothideomycetes unknown (Appendix S1: Table S2). No significant correlations were found with NMS 3.

Root biomass differed among species from 0.07 ± 0.02 g/kg soil in *C. grandiflora* plots to 1.80 ± 0.48 g/kg soil in *P. spicata* plots (Fig. 6; $F_{11,180} = 3.62, P = 0.0001$).

Root biomass did not differ between natives and nonnatives ($t_{1,5} = 1.97, P = 0.08$), though the two dominant natives had greater root biomass than four of the six nonnative species (Fig. 5). Root biomass was not correlated with PSF for all species ($F_{1,11} = 0.00, P = 0.98$), natives ($F_{1,5} = 0.14, P = 0.73$) or nonnatives ($F_{1,5} = 3.08, P = 0.15$). Similarly, root biomass was not correlated with landscape abundance for all species ($F_{1,11} = 0.06, P = 0.80$) or for natives ($F_{1,5} = 0.08, P = 0.80$) or nonnatives ($F_{1,5} = 0.37, P = 0.57$).

Soil penetration resistance differed among species from 1.38 ± 0.29 kg/cm² on *T. dubius* soils to 0.74 ± 0.14 kg/cm² on *P. spicata* soils ($F_{12,86} = 2.07, P = 0.03$; Appendix S1: Table S3). Penetration resistance was not correlated with PSF for all species ($F_{1,12} = 1.17, P = 0.30$), natives ($F_{1,5} = 1.28, P = 0.31$), or nonnatives ($F_{1,5} = 3.08, P = 0.52$). Penetration resistance did not differ between native and nonnative soils ($T_{1,11} = 0.16, P = 0.87$). Penetration resistance was not correlated with landscape abundance for all species ($F_{1,12} = 1.62, P = 0.23$) for natives ($F_{1,5} = 0.14, P = 0.73$) or nonnatives ($F_{1,5} = 0.51, P = 0.15$).

Soil shear strength ranged from 2.43 ± 0.26 kg/cm² on *T. dubius* to 4.15 ± 0.37 kg/cm² on *S. loeselii* soils but there was no difference among species ($F_{12,86} = 1.71, P = 0.08$; Appendix S1: Table S3). Shear strength was not correlated with PSF for all species ($F_{1,12} = 1.27, P = 0.28$), natives ($F_{1,5} = 0.53, P = 0.50$) or nonnatives ($F_{1,5} = 0.14, P = 0.72$). Shear strength did not differ between native and nonnative soils ($T_{1,11} = 1.33, P = 0.21$). Shear strength was not correlated with landscape abundance for

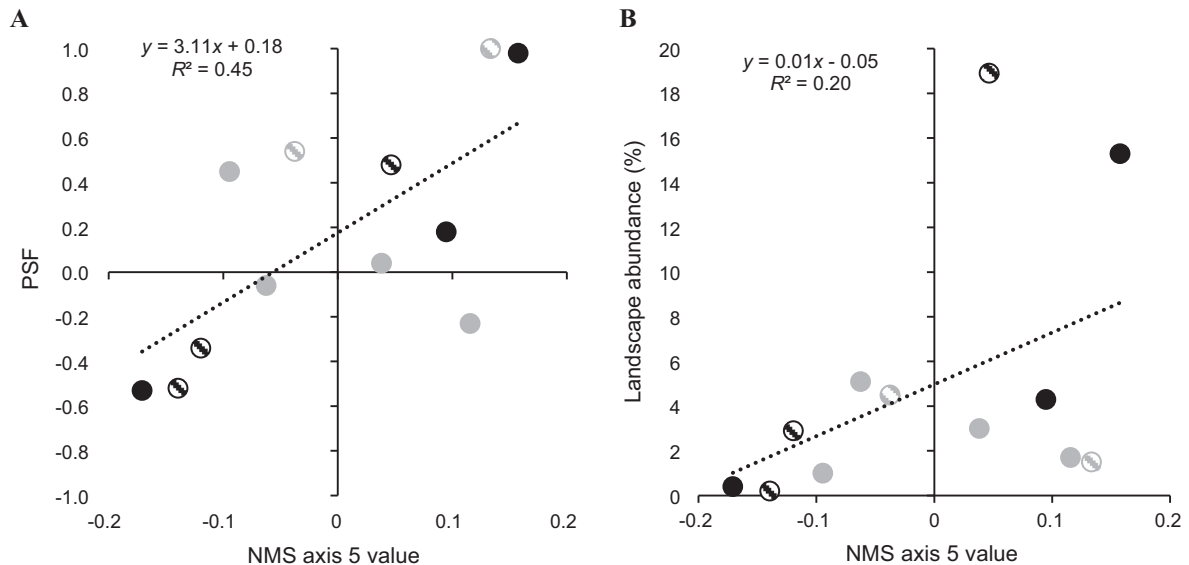


FIG. 4. Scores from NMS axis 5 determined from the microbial community composition vs. (A) plant–soil feedback (PSF) and (B) plant landscape abundance (%). Microbial community composition determined through genetic sequencing of soils from plots in a common garden experiment that were cultivated by different plant species for four years prior to sampling. PSF represents the growth of a plant on self- vs. other-cultivated soils. Black and gray symbols represent soils cultivated by native and nonnative plant species, respectively. Solid and hatched symbols represent forbs and grasses, respectively. See *Methods* for details. Landscape abundance was determined in a separate study (Kulmatiski 2006).

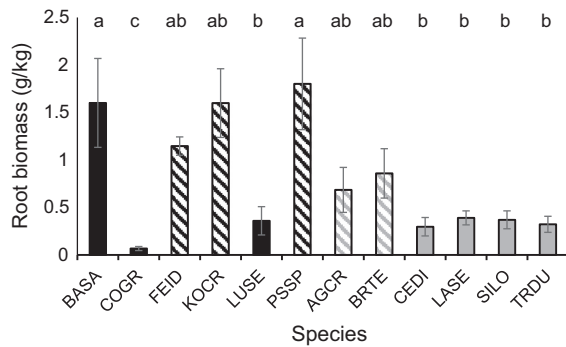


FIG. 5. Root biomass (g/kg) measured in soils cultivated by the indicated species for four years in a common garden experiment, Winthrop, Washington, USA. Black and gray symbols represent soils cultivated by native and nonnative plant species, respectively. Solid and hatched symbols represent forbs and grasses, respectively. Values are mean \pm SE. Bars with different lowercase letters are different at the $\alpha = 0.05$ level. Species codes defined in Table 1.

all species ($F_{1,12} = 0.09$, $P = 0.77$), natives ($F_{1,5} = 0.14$, $P = 0.73$), or nonnatives ($F_{1,5} = 7.92$, $P = 0.83$).

Soil bulk density ranged from 1.03 to 1.19 g/cm³, but no differences were detected among species ($F_{11,180} = 1.25$, $P = 0.26$; Appendix S1: Table S3). Soil bulk density was not correlated with PSF for all species ($F_{1,11} = 3.72$, $P = 0.08$), natives ($F_{1,6} = 3.65$, $P = 0.13$), or nonnatives ($F_{1,5} = 1.23$, $P = 0.33$). Soil bulk density did not differ between native and nonnative soils ($T_{1,10} = 0.39$, $P = 0.71$). Soil bulk density was not correlated with landscape abundance for all species ($F_{1,11} = 2.43$, $P = 0.15$) or for natives ($F_{1,5} = 2.43$, $P = 0.20$) but bulk density was correlated with landscape abundance for nonnatives ($F_{1,5} = 7.92$, $P = 0.05$, $R^2 = 0.66$).

Net N mineralization rates ($F_{11,81} = 2.44$, $P = 0.01$) were smallest under *C. grandiflora* and largest under *C. diffusa* (Fig. 7; Appendix S1: Table S4). Net N mineralization was not correlated with PSF for all species ($F_{1,11} = 0.02$, $P = 0.89$) for natives ($F_{1,5} = 0.39$, $P = 0.56$) or nonnatives ($F_{1,5} = 1.83$, $P = 0.25$). Net N mineralization did not differ between native and nonnative soils ($T_{1,10} = 1.44$, $P = 0.18$) though four nonnatives had greater rates than three natives and no natives had greater rates than any nonnatives (Fig. 6). Net N mineralization was not correlated with landscape abundance for all species ($F_{1,11} = 0.03$, $P = 0.86$), for natives ($F_{1,5} = 0.00$, $P = 0.97$), or nonnatives ($F_{1,5} = 3.07$, $P = 0.15$).

DISCUSSION

After four years in a common garden, the plants in this experiment created soils with different biological, nutrient, and physical traits that changed subsequent plant growth (i.e., PSF). Six of the 13 species grew better on self than control soils indicating positive PSFs. Only three species grew worse on self than control soils. These PSF values were more positive than commonly reported

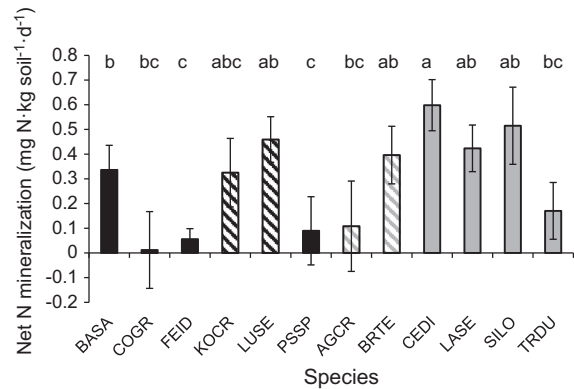


FIG. 6. Net-nitrogen mineralization (mg N·kg soil⁻¹·d⁻¹) measured in soils cultivated by the indicated species for four years in a common garden experiment, Winthrop, Washington, USA. Black and gray symbols represent soils cultivated by native and nonnative plant species, respectively. Solid and hatched symbols represent forbs and grasses, respectively. Values are mean \pm SE. Bars with different lowercase letters are different at the $\alpha = 0.05$ level. Species codes defined in Table 1.

in the literature, but they appear biologically relevant because they correlated positively with native plant abundance on the landscape. Results largely confirm findings from previous studies. More specifically, results supported previous findings that PSFs are more positive for dominant relative to less common species (Klironomos 2002) and longer-lived species relative to shorter-lived species (Kardol et al. 2006), but they provide a rare example from a comprehensive, long-term, field-based PSF experiment (Kulmatiski et al. 2008, van Der Putten et al. 2013, Heinze et al. 2016).

While it is widely accepted that PSF should help determine plant abundance on the landscape, relatively few studies have demonstrated this pattern (Klironomos 2002, Mangan et al. 2010, van Der Putten et al. 2013, Bennett et al. 2017). Here we found a positive correlation between PSF and plant abundance on the landscape, though this reflected a relationship for native and not for nonnative plants. A positive correlation between PSF and plant abundance makes intuitive sense: plants that increase the growth of conspecifics are likely to produce large plants, dense communities and large landscape abundance (Bever et al. 1997, Chisholm and Muller-Landau 2011, Mack and Bever 2014). However, this prediction assumes that PSF effects are large relative to competition effects (Bever et al. 1997, Bever 2003). Because plants are often not competitively equivalent, PSF effects must be large relative to intrinsic differences in growth rates or important relative to other growth factors to affect landscape abundance (Bever et al. 1997, Chisholm and Muller-Landau 2011, Kulmatiski 2016, Kulmatiski et al. 2016). There is no inherent reason that a plant that has intrinsically slow growth rates (e.g., because of large root growth or defenses) would be expected to have negative PSF. Similarly, there is no inherent reason that a plant that has intrinsically fast

growth that allows large ground cover would realize positive PSF. To the contrary, it is more likely that well-defended, slow growing species would realize neutral PSF while poorly defended, fast-growing species would realize negative PSF. Yet, as has been found in other studies (Klironomos 2002, Mangan et al. 2010), we found a positive correlation between PSF and landscape abundance. This suggests either that PSFs were important relative to other plant growth factors or that PSFs covary with other plant traits that are also associated with landscape abundance.

We found that long-lived native plants realized more positive PSF than short-lived native plants. This is consistent with previous research that has found that PSF is correlated positively with plant successional stage (Kardol et al. 2006, Bauer et al. 2015). Further, we found that PSF and landscape abundance covaried (McCarthy-Neumann and Kobe 2008). Several, non-mutually exclusive explanations for these correlations exist. Plants may only be able to attain large ground cover or long lifespans if they realize positive PSF. Alternatively, PSF may, through unknown mechanisms, be a natural consequence of long lifespan or large abundance. These relationships must be considered with caution because they are based on the growth of only seven native plant species. These seven species, however, represent 70% of the total plant cover and 87% of herbaceous plant cover in the surrounding native plant communities so results are important for the study system. Further, the correlation between PSF and abundance, and PSF and lifespan are consistent with results in other ecosystems (Klironomos 2002, Kardol et al. 2006). Together, results from this and previous research suggest that positive PSFs are part of a suite of traits that are important in determining landscape abundance (Klironomos 2002, Casper and Castelli 2007, Mangan et al. 2010). Explaining the mechanisms behind the positive relationship among PSF, lifespan and abundance remains an important direction for research.

PSFs also seemed to be important for nonnative plants, but these species appeared to rely on a different set of traits to attain large abundance on the landscape. Nonnative plants were short-lived and, therefore, were expected to demonstrate negative PSFs (Fig. 7; Kardol et al. 2006, Kulmatiski et al. 2008), yet we did not detect a difference in PSF values between the seven native plants (-0.09 ± 0.25) and six nonnative plants (0.29 ± 0.19). Because PSFs were more positive than would be expected for such short-lived species, it appeared likely that positive PSF was important for the success of nonnatives on the landscape. PSF was not correlated with lifespan for nonnative plants, but this was not surprising because all but one nonnative species had a lifespan less than two years.

Measurements of root biomass and N cycling highlighted other ways in which nonnatives appeared to create plant–soil communities that function in a different way than their native counterparts. Previous research using an observational approach in the study area found

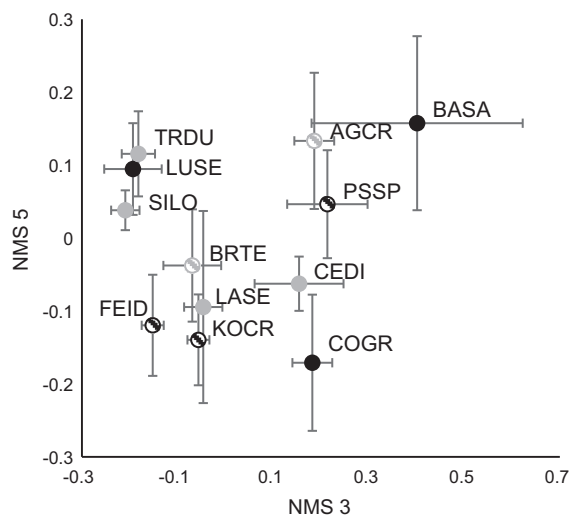


FIG. 7. Lifespan vs. plant–soil feedback (PSF) for seven native plants (native) and six nonnative plants. Data for native plants in black. Data for nonnative plants in gray. The correlation was significant for native but not for nonnative plants.

that nonnative plant communities were associated with faster nutrient cycling (Kulmatiski et al. 2006). Here we found similar patterns with dominant nonnative plants (e.g., *C. diffusa*) creating soils with smaller root biomass and faster net N mineralization rates relative to dominant native plants (e.g., *P. spicata*). Because this study used a common-garden approach, it provided a more controlled test of species effects on N cycling than the previous observational study. Results are consistent with studies in other systems and with the idea that early-successional, weedy species create fast nutrient cycling conditions that benefit their own growth (Hawkes et al. 2005, Chapman et al. 2006, Carol Adair and Burke 2010, Germino et al. 2016, Morris et al. 2016, DeCrappeo et al. 2017, Jo et al. 2017).

While soil penetration resistance and shear strength were not correlated with PSF or landscape abundance, we did observe a negative correlation between soil bulk density and nonnative plant abundance on the landscape. This result was consistent with previous research in a nearby study site, which suggested that fast-growing nonnative plants may encourage their own growth by creating low-density soils (Kyle 2005, Kyle et al. 2007). This result provides a rare test of the role of physical–soil PSF (Bergmann et al. 2016).

Though it is possible for plants to change soil nutrients and soil physical properties in ways that feedback to affect subsequent plant growth (Ehrenfeld et al. 2005, Ke et al. 2015), PSFs are often assumed to reflect plant–microbial interactions (Bever et al. 2013). We found that soil archaeal, bacterial, and fungal communities differed among soils cultivated by different plant species. Further, we found that these differences were correlated with PSFs and plant abundance on the landscape. More specifically, we found that fungal taxa were best correlated with NMS

axis 5 (i.e., R^2 values of 0.19–0.26 for fungi vs. 0.13–0.19 for bacteria), which was itself correlated with PSF and plant abundance. These taxa included one Basidiomycota (Tremellomycetes Filobasidiales) and several Ascomycota (in the Sordariomycetes and the Dothideomycetes). A bacterium in the Planctomycetes Phycisphaerae was also well correlated with NMS 5. Relatively little is known about these organisms in particular, but broadly, the covariation among these taxa, NMS axis 5, PSF, and plant abundance provided clear support for the role of fungal and bacterial PSF in this system. More specifically, our results suggested that plants that were able to increase the abundance of these specific soil organisms were able to increase their own growth and abundance on the landscape: these microbial species appeared to be beneficial to the growth and abundance of the dominant plant species.

Soil chemical and physical properties also differed among soils cultivated by different plant species, but, with the exception of nonnative soil bulk density, were not correlated with PSF or plant abundance on the landscape. As a result, support for the role of nutrient and physical PSF was less clear than it was for microbial PSF. It is certainly possible that none of the relationships reflect causation, but the correlations between microbial parameters and PSF and the lack of correlation between plant chemical or plant physical parameters and PSF suggest that it is more likely that plant–microbe interactions explained observed PSF than plant chemical or plant physical PSF. Alternatively, it is possible that these biological, nutrient, and physical properties interact in important ways that, if described, would provide a better understanding of plant community dynamics.

It is not clear why PSFs were more positive in this experiment than PSFs often reported in the literature (Kulmatiski et al. 2008, Heinze et al. 2016). One potential explanation is that field-based experiments result in more positive PSF than greenhouse experiments (Kulmatiski et al. 2008). One potential reason that field experiments may result in more positive PSFs is that field experiments allow long-lived plants, such as *B. sagittata* and *P. spicata*, to grow for several years and the use of long-lived plants or long growth periods may encourage the development of positive PSF (Kardol et al. 2006). Alternatively, it is possible that greenhouse experiments, which occur in typically warm, wet conditions on young plants, may encourage negative PSF (Kardol et al. 2013, Heinze et al. 2016). As a case in point, results from this field experiment stand in contrast to a recent greenhouse-based study with some of the same species in a nearby ecosystem. That study found generally negative PSF and a negative correlation between plant abundance on the landscape and PSF (Maron et al. 2016). Yet another possible explanation for positive PSF in this field experiment is that larger and more diverse soil communities that included larger soil organisms and higher trophic levels may have encouraged greater plant growth and more positive PSFs (Latz et al. 2012, Kulmatiski et al. 2014). Finally, it is

possible that the self vs. control approach used here may produce more positive PSF estimates than other common self vs. other approaches (Kulmatiski et al. 2008, Brinkman et al. 2010). It is possible, for example, that mycorrhizal abundance decreased over time in the control plots where vegetation was removed and early-successional species that are often non-mycorrhizal (e.g., Brassicaceae) were common. Relatively low mycorrhizal abundance in control soils could be expected to result in positive feedbacks if species increased mycorrhizal abundance in self relative to control soils.

Taken together, results from this relatively long-term field experiment described a native plant community dominated by long-lived plants with positive microbial-driven PSF, large root biomass, and slow N cycling and a nonnative plant community dominated by short-lived plants with unexpectedly positive PSF, small root biomass, and fast N cycling. With measurements of dominant plant effects on soil biological, chemical, and physical traits in a long-term field experiment, results provide a comprehensive perspective on PSFs in the study system. Results (1) suggest that PSFs may be more positive than suggested from greenhouse studies, (2) provide an example of a correlation between PSF and plant abundance on the landscape, (3) further support the idea that nonnative plants escape belowground enemies, (4) demonstrate a correlation between plant lifespan and PSF, and (5) suggest that plant–microbe PSF are more important than plant–nutrient or plant–physical feedbacks. However, while results provide insight into the dominant species in the study ecosystem, results must be taken with caution because a large number of potential correlations were examined using a relatively small number of species and because correlations with 6–13 species are potentially spurious.

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