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Improving rotational partners: Intraspecies variation for pea cover cropping traits

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To improve cover crops such as peas (*Pisum sativum*), as rotational partners, intraspecific variation for cover cropping traits such as nutrient mobilization, carbon deposition, and beneficial microbial recruitment must be identified. The majority of research on cover crops has focused on interspecies comparisons for cover cropping variation with minimal research investigating intraspecies variation. To address if variation of cover cropping traits is present within a cover cropping species, we grew 15 diverse accessions (four modern cultivars, three landraces, and eight wild accessions) of pea in a certified organic setting. We measured various cover cropping traits, such as nutrient mobilization, soil organic matter deposition, and microbial recruitment, and quantified the effect of pea accession on the growth and yield of a subsequently planted crop of corn (*Zea mays*). We discovered that the domestication history of pea has a significant impact on soil properties. Specifically, domesticated peas (modern cultivars and landraces) had higher average plant–soil feedback values for amounts of nitrogen, carbon, and manganese compared to wild peas. Additionally, no variation for prokaryotic recruitment (α- and β-diversity) was observed within pea; however, we did observe significant variation for fungal recruitment (α- and β-diversity) due to domestication and accession. Our results demonstrate that there is variation present in peas, and likely all crops, that can be selected to improve them as rotational partners to ultimately boost crop yields in sustainable agroecosystems.

1 | INTRODUCTION

Cover crops are widely recommended in agricultural systems due to their beneficial impacts on crop yields, above and belowground biodiversity, disease and weed suppression, and soil properties (e.g., Barbieri et al., 2019; Blanco-Canqui & Ruis, 2020; Hartwig & Ammon, 2002; Licker et al., 2010; Miguez & Bollero, 2005; Ponisio et al., 2015; Sharma et al., 2018; Snapp et al., 2005). The majority of cover crop research has been focused on comparing cover cropping traits among species or species mixtures, whereas few studies have investigated differences in cover cropping traits within species (e.g., Blanco-Canqui & Ruis, 2020; Florence and McGuire, 2020; Osipitan et al., 2018; Sharma et al., 2018). Identifying intraspecies differences may provide the foundation for improving the rotational value of cover crops, which we define as a measure of how well a cover crop increases the yield of a subsequent crop (Marques et al., 2020). To this end, increasing rotational value may potentially help offset the estimated

Abbreviations: ASV, amplicon-sequence variants; CEC, cation exchange capacity; PSF, plant–soil feedback; SM, soil measurement.

approximately 20% yield gap between conventional and sustainable agricultural practices (Ponisio et al., 2015; Sharma et al., 2018) and the relatively low uptake of cover cropping among the majority of farmers (e.g., https://www.sare.org/publications/cover-crops/national-cover-crop-surveys/).

Many species have been utilized as cover crops, from cereals like rye (*Secale cereale*) and triticale (×*Triticosecale* Wittmack), and legumes like hairy vetch (*Vicia villosa*), kura clover (*Trifolium ambiguum*), and field peas (*Pisum sativum*). Differences in cover cropping traits among species and families, including weed and disease suppression (Snapp et al., 2005), soil organic matter deposition (Johanning, 2014), nutrient mobilization (Hallama et al., 2019), and belowground (Liang et al., 2014; Wagg et al., 2011) and aboveground (Finney & Kaye, 2017) biodiversity improvement, have been well documented in various agroecosystems (Hartwig & Ammon, 2002; Sharma et al., 2018). For instance, when compared to cereal cover crops, legume cover crops are not well suited for weed suppression (Chauhan et al., 2012; Hodgdon et al., 2016) but are more efficient at increasing soil nitrogen (Snapp et al., 2005). Despite these well-established cover crop generalizations, most cover cropping studies are limited in that they use a single variety or accession to represent an entire cover cropping species. The use of a single accession or variety is problematic because within-species variation for agronomically important traits, such as abiotic tolerance (e.g., Bita & Gerats, 2013; Bosetti et al., 2012), and resistance to diseases (Ahmad et al., 2010; Vasudevan et al., 2014) and pests (Broekgaarden et al., 2011; Rakha et al., 2017) have been consistently found across crops. As a result, intraspecific variation for cover cropping traits such as nutrient mobilization, organic matter deposition, and beneficial soil microbial recruitment most likely exists but to the best of our knowledge are rarely if ever tested. Therefore, cover cropping results from a single variety or accession must be carefully extrapolated since it may lead to incorrect generalizations about crop families or species.

In addition to increasing the number of accessions and varieties used in studies, crop wild relatives (CWRs) should be incorporated in cover cropping research. Tribouillois et al. (2015) suggested that domestication has reduced adaptive strategies and modified leaf trait syndromes in cover crops. Thus, the impacts of genetic bottlenecks associated with domestication and modern breeding (Khoury et al., 2022) may also be affecting the genetic and phenotypic diversity of cover crops. To alleviate restrictions on genotypic and phenotypic diversity, incorporating genetic material from CWRs that have not undergone domestication may help increase intraspecies variation in cover cropping studies.

Here, we test if rotational traits and values vary within cover cropping species by utilizing a modified plant–soil feedback (PSF) framework (Marques et al., 2020) and an assortment of pea accessions with varying domestication histories (modern cultivars, landraces, and wild relatives). We measured various cover cropping traits, such as nutrient mobilization, organic matter deposition, microbial recruitment, and rotational values. We hypothesized that cover cropping traits would vary among pea accessions and domestication histories. We specifically expected to see higher variability in cover cropping traits in wild pea accessions compared to domesticated accessions, as other agronomically important traits have been seen to vary among pea accessions (e.g., Coyne et al., 2020). The presence of variation in cover cropping traits would suggest that rotational values in cover crops can be enhanced to increase yields in agroecosystems.

Core Ideas

- Crop rotation value is the impact one crop has on the subsequent crop mediated by plant-soil feedback.
- Intraspecific variation in rotational value traits likely exists in many crops.
- Cover crops are selected to improve the yield of subsequent crops, yet very few studies on cover crops have examined the intra-specific variation in traits that confer rotational value that breeders could select to make cover crops better at being cover crops.

2 | METHODS

2.1 | Plant material

Fifteen pea accessions were used in this experiment. All accessions were requested from the USDA-NPGS and then underwent a generation of seed increase by selfing in a greenhouse in Burlington, VT. Eight of the accessions, W6 26154, W6 26154 PSP, W6 26157, W6 26157 PSP, W6 26159, W6 26160 PSP, W6 26161, and W6 26161 PSP, were wild accessions from the country of Georgia. The remaining accessions, PI 269761, PI 269761 PSP, PI 639977 PSP, and PI 639981 PSP, were modern cultivars originating from the Czech Republic (2) and Bulgaria (2), respectively, and PI 577142, W6 3674, and W6 3675 were landraces from Nepal (Table S1).

2.2 | Experimental design

Four replicates of each pea accession and one control (no cover crop) were grown in a randomized block design in a

certified organic field at the University of Vermont Horticulture Research Center in South Burlington, VT (44.431893, −73.205270). The soil type is Adams Windsor loamy sand, part of the ancient shore of Lake Champlain. The field had been used for diversified organic vegetable production for the 5 prior years, with tomatoes the year prior and peas 3 years before. Approximately 20.41 g of each pea accession was planted at a depth of ∼2.54 cm in 2.8 m^2 plots. The sowing rate of ∼7.3 g/m^2 and the 2.54 cm planting depth mimicked the recommended cover cropping plant density of 72.86 kg/ha for cover cropping peas (Berg et al., 2017; USDA, 2019). Before planting, all seeds were sterilized with a 1% bleach solution to ensure no microbes were introduced to the plot via the seed coat. Seeds were not inoculated with rhizobia to allow for differential nodulation with resident rhizobia, which we expected to be present based on sweet peas having been produced on the plots within the past 5 years. We elected to not inoculate based on evidence that grain legumes like chickpeas (Greenlon et al., 2019) and peas (Smykal et al., unpublished; Porter et al., unpublished) differ in the benefit they gain from particular rhizobial strains, and the fact that recent planting of inoculated peas in the field should have created a resident population of rhizobia in the soil. Plots were irrigated once to establish the peas and once to establish the corn (see below) and did not require further irrigation. Pea plants were sown with an Earthway seeder on December 05, 2018 (11˚C) into plots of 1.2 m by 2.1 m with 2.5 cm spacing. And were grown for 44 days, after which soil rhizosphere samples were collected, and the total number of plants in the plot, the average plant height, and the average aboveground biomass were recorded. To calculate the average plant height, three of the most center plants (that were representative of the entire plot) in the plot were selected, and plant height (base of the plant at soil level to the top of the stem) was recorded and averaged. Three were chosen to minimize edge effects and disturbance to the plots. The plants were uprooted gently with a trowel after their height was measured, and soil rhizosphere samples were collected. The rhizosphere was defined as any soil still clinging to the plant's root after the plant was uprooted. For control plots, bulk soil was taken at an approximate depth of 15 cm at the center of the plot. To calculate the average aboveground biomass, the three uprooted plants' aboveground portions were separated from their belowground portions and oven-dried for 48 h at 49˚C and then weighed using an analytical scale. After pea plant measurements were recorded, soil core samples were collected at the center of each plot at an approximate depth of surface to 15 cm using a 7.5-cm diameter soil recovery AMS auger. Soil samples and the previously listed plant measurements were obtained from the plots' centers to avoid edge and interacting effects from neighboring plots. Soil core samples were then sent to the University of Vermont Agricultural and Environmental Testing Laboratory (https://www.uvm.edu/extension/agricultural-and-environmental-testing-lab), where they were tested for pH, nitrogen (N) (g/kg), carbon (g/kg) I, percent soil organic matter, phosphorus (mg/kg), potassium (mg/kg), aluminum (mg/kg), calcium (mg/kg), iron (mg/kg), magnesium (mg/kg), manganese (mg/kg), sulfur)mg/kg), zinc (mg/kg), and effective cation exchange capacity (CEC). Total C and N were quantified using the gas chromatography-thermal conductivity detector method, while both macro- and micronutrients were measured using the modified Morgan soil test method. Organic matter content was determined using the Walkey–Black method and the loss-on-ignition method, while pH was measured using the saturated paste extract method. After the soil core samples were obtained, the remaining plots were hand-harvested by cutting the plant's stem at the soil level; this was done to minimize soil disturbance in the plot. We decide not to return the pea aboveground biomass to the soil for fear with would cause too much disturbance to the subsequent planting of corn. It is not unusual for some farmers to use the aboveground biomass of a cover crop as supplemental feed instead of returning it to the soil in Vermont.

After harvesting pea plants, the sweet corn (*Zea mays*) organic variety Enchanted was hand planted in the plots according to the New England Vegetable Management Guide (https://nevegetable.org/). Enchanted was used because it is a neonicotinoid-free and late-season maturing variety that reaches maturity 78 days after sowing. No fertilizer was added to the corn to test the impact of the prior pea crop. Eighty days after sowing, the number of corn plants, average plant height, average aboveground biomass (cob and vegetative), and relative chlorophyll content were recorded for each plot (explained in more detail below). The same protocol used to calculate the average plant height and aboveground biomass of the pea plants was used for the corn plants. If a cob showed signs of pest damage, the measurement for that plant was excluded, and another plant in the plot was measured. For chlorophyll measurements, the youngest fully developed leaf was measured for leaf chlorophyll content using a Leaf Photosynthesis MultispeQ V1.0 (East Lansing, MI). Only plants closest to the direct center of the plot were sampled to avoid edge and interacting effects from neighboring plots.

2.3 | Microbiome measurements

Microbial DNA was extracted from bulk soil control plots and pea rhizosphere samples using QIAGEN DNeasy PowerSoil Kits. Before DNA extraction, all samples were treated with propidium monoazide utilizing the manufacturer's protocol (Biotium) to prevent the extraction and amplification of soil relic DNA, which can potentially skew microbial diversity estimates (Carini et al., 2016). After extraction, DNA samples

were sent to LC Sciences for DNA library preparation, and sequenced for prokaryotic 16S rRNA (V3 and V4 regions) and internal transcribed spacer genes using an Illumina MiSeq sequencer. Only one rhizosphere sample from each plot was sequenced. Sequence data were then processed for amplicon-sequence variants (ASVs) using the requisite quality assurances in the Qiime2 and Dada2 pipelines (Callahan et al., 2016). The taxonomy of the ASVs was characterized using the Ribosomal Database Project (RDP version 11.3), NCBI 16S Microbial Database, and the Greengenes databases.

2.4 | Statistical analysis

To calculate the effect of pea accessions on soil chemistry and the growth of the subsequently planted corn, a modified PSF framework was used, and the magnitude and direction of PSF in each accession were calculated for all measurements (Ingerslew & Kaplan, 2018; Mariotte et al., 2018; Marques et al., 2020). For all measurements, the following formula was used:

$$\mathrm{PSF} = \ln\left(\frac{\mathrm{SM_s}}{\mathrm{SM_c}}\right)$$

where $\mathrm{SM_s}$ is the recorded soil measurement (SM) or corn measurement of the plot, and $\mathrm{SM_c}$ is the average soil or corn measurement for all control plots. Additionally, the same metric was used to calculate the rotational value (RV), where $\mathrm{SM_s}$ is the average corn cob weight of the plot, and $\mathrm{SM_c}$ is the average corn measurement of all control plots. The use of a standardized PSF and RV measures a pea accessions' effect on soil chemistry and the subsequently planted crop. If PSF or RV was <0, soil or corn measurements were lower than control measurements. If PSF or RV was >0, soil or corn measurements were higher than control measurements. Lastly, if PSF or RV was equal to 0, then soil or corn measurements were similar to control measurements.

A generalized linear mixed model was used to test for significant differences among accessions and histories (modern cultivar, landrace, and wild) effects on soil chemistry and corn growth and yield (Bates et al., 2014). For SM GLM models, block was used as a random variable, and the total aboveground biomass of the plot was used as a covariate. The total aboveground biomass of the plot was calculated by multiplying the number of pea plants in the plot by the average pea aboveground biomass of the plot. Although not a precise measure, this proxy gave an approximate estimate of the total aboveground biomass of the plot while minimizing disturbance. This covariate was used to account for differences in pea plant size among accessions. For corn measurement GLM models, block was again used as a random variable, and the number of corn plants in the plot was used as a covariate. This covariate was used to account for differences in the number of corn plants present in each plot. A Tukey's honest significant difference (HSD) post hoc test was used to test for significant differences among accessions and history groups. The effects of accession and history (domesticated or wild) on soil and corn measurements were analyzed separately, as we wanted to test for significant differences among accessions. If both factors were included in a single model, accession would become nested within history and be categorized as a random term, thus preventing the identification of significant differences among accessions.

To test for linear correlation between rotational value and PSF soil calculations and pea measurements, the Pearson correlation coefficient was calculated for rotational values versus pea measurements or PSF soil calculations. Additionally, to test for linear correlation between pea aboveground biomass of the plot and SMs, the Pearson correlation coefficient was calculated for all PSF soil calculations versus pea aboveground biomass. All statistical analyses were performed in R (www.r-project.org).

2.5 | Microbial analysis

ASVs were rarefied to 90% of the minimum sample depth in the dataset. Rarefied ASVs were used to calculate α-diversity for both history and accessions using Chao1, Shannon, Simpson, abundance-based coverage estimators, and Fischer indices. α-diversity was calculated using the "Phyloseq" and the "microbiomeSeq" R packages. A one-way (accession or history) analysis of variance and a Tukey's HSD post hoc test were used to determine if alpha microbial diversity was significantly different among accessions and history groups. Additionally, the Bray–Curtis dissimilarity method with a Hellinger transformation was used to calculate β-diversity for accession and history. The dissimilarity matrices were then analyzed with distance-based redundancy analysis (db-RDA) and permutational multivariate analysis of variance (PERMANOVA). All β-diversity analysis was conducted using the "Vegan" package and RDA graphs were made using the "ampvis2" package in R. Furthermore, using the "Vegan" package in R, a redundancy analysis was performed to calculate the amount of variation present in species explained by accession history, respectively. To test for differential abundance of ASVs for accessions, the "differentialTest" function (controlling the effect of domestication history on dispersion) from "Corncob" package in R was used (Martin et al., 2020). Lastly, to test for linear correlation between rotational values and prokaryotic and fungal presence at the phylum level, the Pearson correlation coefficient was calculated for rotational values versus all normalized microbial groups using R's "psych" package. Prokaryotic and fungal communities were analyzed separately.

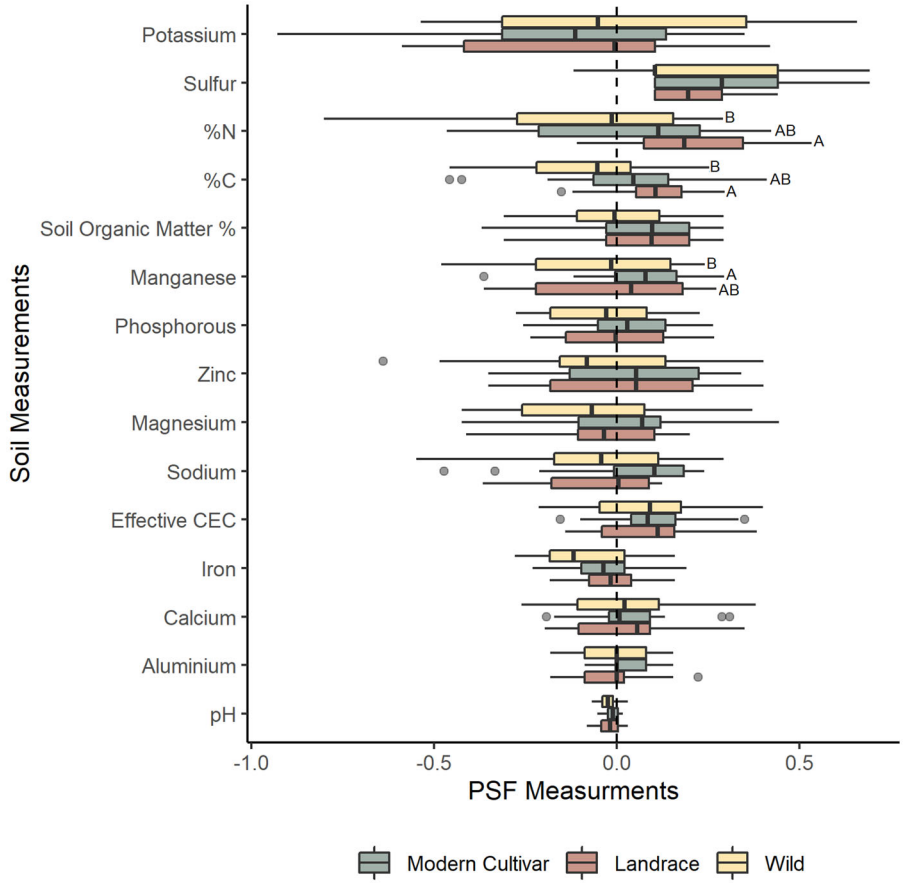

FIGURE 1 Plant–soil feedback (PSF) soil measurements by domestication history (modern cultivar, landrace, and wild). Letters indicate significant difference within soil measurement at the $p < 0.05$ level. If letter is not present, it indicates non-significance from all other groups.

3 | RESULTS

3.1 | PSF values of SMs

The PSF values of soil chemistry measurements varied among modern cultivars, landraces, and wild peas, with modern cultivars and landraces generally having positive or neutral values and wild peas having negative or neutral values (Figure 1). Significant differences in PSF values for nitrogen ($p = 0.016$), carbon ($p = 0.046$), and manganese ($p = 0.044$) were observed among modern cultivars, landraces, and wild peas, with domesticated (modern cultivar, landraces) peas having higher PSF values than wild peas (Figure 1). Conversely, for potassium ($p = 0.110$), the PSF value of wild peas trended higher than modern cultivars, but not significantly so. For all other measurements, pH ($p = 0.195$), magnesium ($p = 0.086$), iron ($p = 0.073$), phosphorus ($p = 0.099$), organic matter ($p = 0.095$), calcium ($p = 0.515$), sulfur ($p = 0.162$), zinc ($p = 0.433$), sodium ($p = 0.174$), aluminum ($p = 0.722$), and CEC ($p = 0.419$) were non-significant with domestication history.

Similar to domestication history, accession variation of soil PSF values was widespread, with accessions having positive, negative, or neutral values (Figure 2). Accessions varied significantly in PSF values for calcium ($p = 0.013$), magnesium ($p = 0.002$), manganese ($p = 0.016$), sodium ($p = 0.007$), CEC ($p = 0.012$),and carbon ($p < 0.001$) (Figure 2). However, accessions did not significantly differ in PSF values for nitrogen ($p = 0.060$), pH ($p = 0.265$), organic matter ($p = 0.304$), phosphorus ($p = 0.203$), potassium ($p = 0.069$), aluminum ($p = 0.089$), iron ($p = 0.371$), sulfur ($p = 0.094$), and zinc ($p = 0.078$).

Additionally, the aboveground biomass of wild and domesticated plants significantly affected soil PSF values for pH ($p = 0.010$), potassium ($p = 0.035$), and magnesium ($p = 0.007$). However, only a significant negative correlation between pH and total aboveground biomass ($r = -0.263$, $p = 0.042$) and a non-significant negative correlation between magnesium and total aboveground biomass ($r = -243$ and $p = 0.062$) were observed. All PSF values are given in Table S2.

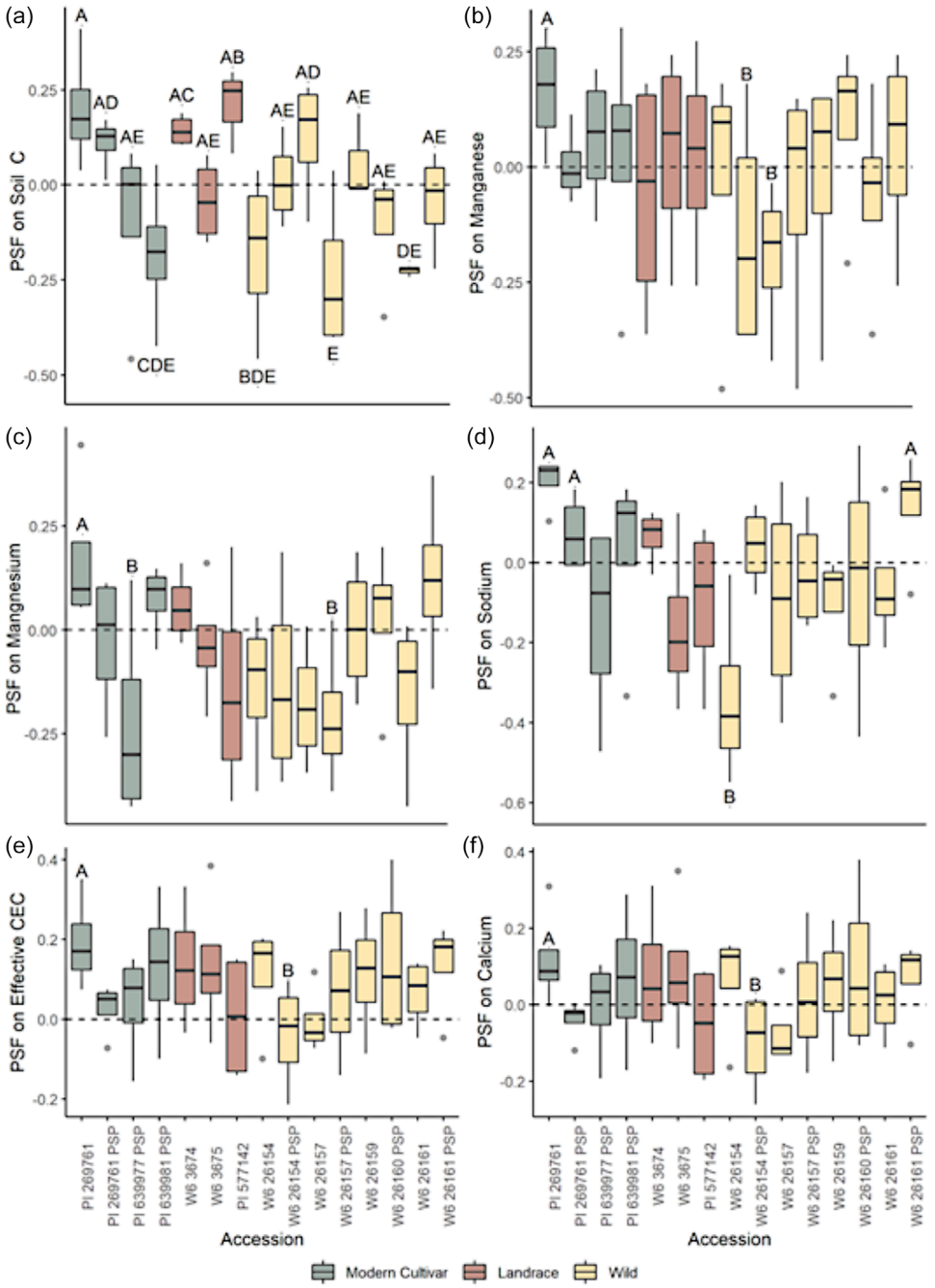

FIGURE 2 Plant–soil feedback (PSF) soil measurements by accession (colored by domestication history, modern cultivar, landrace, and wild) for (a) carbon, (b) manganese, (c) magnesium, (d) sodium, (e) effective cation exchange capacity (CEC), and (f) calcium. Letters indicate significant difference within soil measurement at the $p < 0.05$ level. If letter is not present, it indicates non-significance from all other groups.

3.2 | Recruited rhizosphere communities

3.2.1 | Prokaryotic communities

α-diversity indices Chao1 ($p = 0.433$ and $p = 0.805$), Shannon ($p = 0.213$ and $p = 0.638$), Simpson ($p = 0.311$ and $p = 0.117$), abundance-based coverage estimators ($p = 0.487$ and $p = 0.825$) and Fisher ($p = 0.383$ and $p = 0.805$) were non-significant for prokaryotic rhizosphere communities for both domestication history and accession, respectively (Figure S1). Additionally, β-diversity (Bray–Curtis dissimilarity) among accessions (PERMANOVA, $p = 0.958$) was not significantly different. However, β-diversity for domestication history (PERMANOVA, $p = 0.059$) was significant at $\alpha = 0.075$. Furthermore, db-RDA revealed that domestication history accounts for 78.9% (RD1 55.7% and RD2 23.2%) of the variation found in the prokaryotic microbiome (Figure 3a).

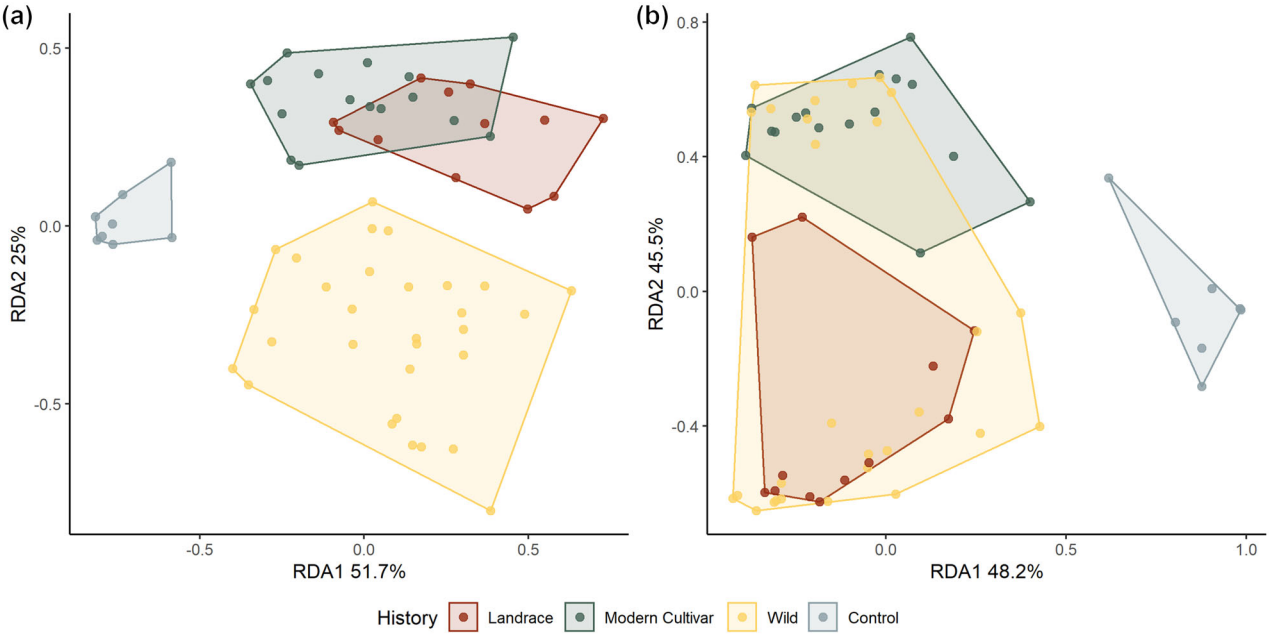

FIGURE 3 Redundancy analysis of species composition by domestication history (modern cultivar, landrace, wild, and control) for (a) prokaryotic and (b) fungal communities. RDA, redundancy analysis.

Lastly, significant differences among accessions for differential abundance were observed for 10 ASV, unclassified Gemmatimonadetes (ASV 20 and $p = 0.03$), unclassified Microvirga (ASV 68 and $p < 0.001$), unclassified Methloligellacea (ASV 116 and $p = 0.03$), unclassified Rhodomicrobium (ASV 164 and $p < 0.001$), unclassified Acidobacteria (ASV 202 and $p = 0.01$), unclassified Neo-b11 (ASV 355 and $p = 0.04$), unclassified C0119 (ASV 581 and $p = 0.03$), unclassified Planctomycetes (ASV 742 and $p = 0.04$), unclassified Omnitrophicaeota (ASV 1056 and $p = 0.03$), and unclassified Omnitrophicaeota (ASV 3775 and $p = 0.03$). Generally, landraces and wild relatives were found to be enriched with unclassified Methloligellacea (ASV 116), unclassified Rhodomicrobium (ASV 164), and unclassified Planctomycetes (ASV 742), when compared to modern cultivars. While modern cultivars and wild relatives were generally enriched with unclassified Omnitrophicaeota (ASV 3775) when compared to landrace accessions. Lastly, wild relative accessions were generally enriched with unclassified Gemmatimonadetes (ASV 20), unclassified Acidobacteria (ASV 202), unclassified Neo-b11 (ASV 355), and unclassified C0119 (ASV 581) when compared to landraces and modern cultivars.

3.2.2 | Fungal communities

For fungal rhizosphere communities, α-diversity, Shannon ($p < 0.001$ and $p = 0.001$), and Simpson ($p = 0.001$ and $p = 0.013$) indices were significant for both domestication history and accession, whereas Fisher ($p = 0.035$ and $p = 0.279$) index was only significant for domestication history. Abundance-based coverage estimators ($p = 0.692$ and $p = 0.597$) and Chao1 ($p = 0.692$ and $p = 0.597$) indices were non-significant for both domestication history and accession, respectively (Figure S2). Additionally, β-diversity (Bray–Curtis dissimilarity) among accessions (PERMANOVA, $p < 0.001$) and domestication history (PERMANOVA, $p < 0.001$) was significant at $\alpha = 0.05$. Furthermore, db-RDA analysis revealed that domestication history accounts for 93.7% (RD1 48.2% and RD2 45.5%) of the variation found in the fungal microbiome (Figure 3b).

Lastly, significant differences among accessions for differential abundance were detected for a single ASV, unclassified *Mortierella* (ASV 11, $p < 0.001$), with landraces generally having higher enrichment than wild and modern cultivars.

3.3 | PSF and rotational values for corn measurements

The PSF values for wild and domesticated peas on corn productivity were widespread with positive, negative, or neutral values (Figure S3). Despite the present variation among wild and domesticated peas, rotational values for cob weight ($F_{1,50} = 3.036$ and $p = 0.088$), vegetative weight ($p = 0.355$), plant height ($p = 0.859$), and chlorophyll content for newest ($p = 0.567$) and oldest ($p = 0.729$) leaf were non-significant between wild and domesticated peas. Similarly, accession PSF values varied with positive, negative, or neutral values.

However, rotational values of cob weight were significantly different among accessions ($p = 0.021$), with accessions W6 26154 PSP (wild) and PI 577142 (domesticated) having the two highest rotational values (Figure 3). Vegetative weight ($p = 0.328$), plant height ($p = 0.874$), and chlorophyll content for newest ($p = 0.849$) and oldest ($p = 0.338$) leaf were non-significant among accessions.

Rotational value was significantly correlated with several cover cropping measurements. Iron ($r = 0.333$ and $p = 0.014$) was the only PSF soil calculation that was positively correlated with rotational value. Nitrogen was not significantly associated with PSF, despite the expectation that legumes provide rotational value through nitrogen and that nitrogen levels in the soil were low for corn production. Additionally, the total aboveground biomass ($r = 0.357$ and $p = 0.007$) of the plot was the only pea aboveground measurement significantly correlated with rotational value. Furthermore, the presence of three prokaryotic phyla was significantly positively correlated with rotational value: *Gemmatimonadetes* ($r = 0.356$ and $p = 0.008$), *Armatimonadetes* ($r = 0.311$ and $p = 0.022$), and *Planctomycetes* ($r = 0.290$ and $p = 0.033$).

4 | DISCUSSION

The main aim of this study was to determine if variation in cover cropping traits and rotational value exists within pea. Our data revealed that the domestication history of pea had a significant impact on soil properties. Specifically, domesticated peas (modern cultivars and landraces) had higher PSF values for nitrogen, carbon, and manganese compared to wild peas. However, wild peas had higher PSF values for potassium compared to modern cultivars. Additionally, we found that pea accession also had a significant effect on soil PSF values, including carbon, nitrogen, manganese, magnesium, sodium, calcium, effective CEC, and the yield of the subsequent corn crop. Therefore, our results indicate that the genotype of a cover crop could have an underappreciated effect on soil properties and the yield of a subsequently planted crop. However, this study's limitations must be considered, as this experiment took place at a single site over one cover cropping season. Therefore, gene–environment interactions and soil legacy effects, which have been seen to influence plant physiology, could have had an impact on our findings (Detheridge et al., 2016; Huang et al., 2013; Wang et al., 2017). Future multi-site and multi-year trials would be needed to determine whether the results obtained in this study were field-specific or not. Despite these limitations, our findings are novel as they illustrate that crops could be improved as rotational partners, highlighting the use of wild relatives and diverse landraces as a phenotypic reservoir for crop improvement.

4.1 | PSF and domestication history

PSF measurements were significantly influenced by domestication, with modern cultivars and landraces, increasing macro- (percentage carbon and nitrogen) and micronutrients (manganese) in the soil relative to the control plots (Figure 1). When focusing on the accession level, significant differences were also observed for macro- (soil carbon and nitrogen, calcium, and magnesium) and micronutrients (manganese and sodium) among accessions (Figure 2). These results are not surprising since cover cropping pea has been previously shown to increase the presence of macro- and micronutrients in soil, with legumes being proficient at increasing soil nitrogen and carbon (McDaniel et al., 2014). Additionally, Mwafulirwa et al. (2016) noted differences in carbon deposition for barley genotypes. However, this is the first time—to our knowledge—that differences in these benefits have been described for pea. Overall, these results indicate that pea could be bred to improve soil properties in agroecosystems.

Recruited prokaryotic communities did not differ in α-diversity between domesticated and wild peas at the history or accession levels. This was expected, as previous studies have shown a nonsignificant difference in α-diversity between CWRs and their domesticated counterparts (Pérez-Jaramillo et al., 2016, 2017). Additionally, β-diversity and differential abundance analysis revealed that pea rhizospheres of domesticated and wild accessions were not significantly different ($\alpha = 0.05$) from each other. These results were unexpected, as a previous meta-analysis revealed β-diversity and enrichment differences in differential abundances between wild and domesticated barley (*Hordeum vulgare*), lettuce (genus *Lactuca*), common bean (*Phaseolus vulgaris*), and hairy bittercress (*Cardamine hirsuteuta*) (Pérez-Jaramillo et al., 2017). Pérez-Jaramillo et al. (2017) concluded that wild relatives' rhizospheres were enriched with *Bacteroidetes*, while their domesticated counterparts were enriched with *Actinobacteria* and *Proteobacteria*. The disparity between our study's results and previous findings could stem from differences in environments (Fierer, 2017; Fierer & Jackson, 2006) and land management practices (Qiao et al., 2017), which have been shown to have stronger effects on soil microbial communities than plant genotypes. Additionally, the lack of significance for β-diversity and differential abundances among pea accessions could have resulted from the limited number of accessions used in this study as it may not have fully captured the entire genetic or phenotypic diversity of microbial recruitment in pea.

Despite finding nonsignificant differences for prokaryotic recruitment within pea, we did observe significant differences in α- and β-diversity for recruited fungal communities due to domestication and accession. Our results agree with Brisson et al. (2019) and Favela et al. (2021), which revealed that

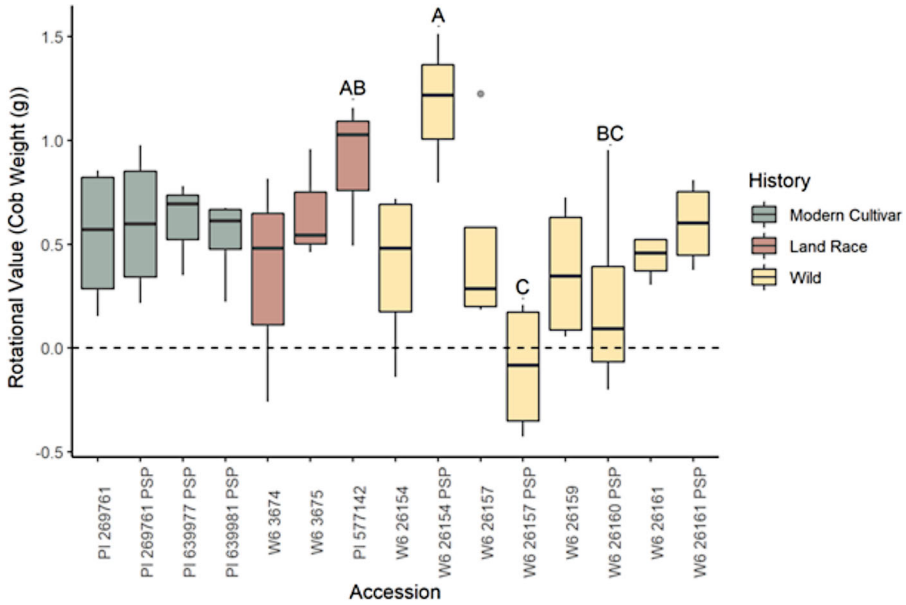

FIGURE 4 Rotational value measurements by accession (colored by domestication history, modern cultivar, landrace, and wild). Letters indicate significant difference within soil measurement at the $p < 0.05$ level. If letter is not present, it indicates non-significance from all other groups.

domestication and breeding have impacted maize rhizosphere microbial community recruitment. However, Chartrel et al. (2021) found differences in α- (observed and Shannon) and β-diversity (Bray–Curtis dissimilarity) in pea due to country of origin (France, Sweden, Canada, all modern cultivars), with peas originating from Canada being more dissimilar to those than France and Sweden. Therefore, country of origin might influence pea microbial recruitment in our study; however, we cannot distinguish this effect as it is nested within domestication history. In total, our results demonstrate that domestication and breeding may have impacted pea rhizosphere fungal communities, and further support the case for utilizing diverse wild relatives and landraces from different country of origins in breeding programs (e.g., Coyne et al., 2020; Gopal & Gupta, 2016).

4.2 | Rotational value

The effect of accession and domestication history of a previously planted pea cover crop on a subsequently planted crop was limited, with nonsignificant differences found for plant height, chlorophyll content, and aboveground biomass. However, pea genotype did significantly influence rotational values of corn yield (cob weight). Accessions W6 26154 PSP (wild) and PI 577142 (domesticated) had the two highest average rotational values (Figure 4). This may, in part, be due to these accessions having neutral and the second-highest PSF carbon measurements, respectively (Figure 2). Additionally, accession W6 26157 PSP had the lowest rotational value and the lowest PSF soil carbon measurement. On average, legume cover crops have been shown to increase soil carbon by ~25%, the highest soil carbon increase of all cover crops (Austin et al., 2017). Moreover, long-term rotations, including pea and spring wheat rotations, increase total soil carbon and grain yields more effectively than shorter rotation combinations and those lacking legumes (Sainju et al., 2017). More importantly, studies have shown that soil carbon is positively correlated with yields in agroecosystems (Lal, 2004; Sainju et al., 2017). However, in our single-season study, PSF total soil carbon percent was not positively correlated with rotational value, which may be due to the length of our study or the approaches we used to measure carbon. Implementations of cover crops over multiple seasons have been shown to have a more profound effect on soil organic carbon and soil organic matter, which contribute to total soil percent carbon measurements (Austin et al., 2017; Olson et al., 2014; Poeplau & Don, 2015). Furthermore, the type of carbon inputs matter, and we were not able to measure multiple soil carbon pools. Nonetheless, our results do suggest that the manipulation of soil carbon may have an integral role in determining the rotational value of accessions.

Rotational value was moderately positively correlated with several cover cropping measurements, one of which was the level of iron. Iron is an essential micronutrient with strong effects on plant growth and yield due to it being a prerequisite for many cellular functions, such as photosynthesis, respiration, enzyme cofactors, redox reagent, and amino acid synthesis (reviewed in Govindaraj et al., 2011; Kumar et al., 2017). Therefore, a correlation between rotational value and iron was not surprising. Additionally, rotational value was moderately positively correlated with

the presence of three prokaryotic phyla, *Gemmatimonadetes*, *Armatimonadetes*, and *Planctomycetes*. *Gemmatimonadetes* may increase rotational value by suppressing diseases, as it has been significantly negatively correlated with bacterial wilt infection rates in tomato (Zhang et al., 2020) and *Fusairum* wilt in banana (Fan et al., 2022; Shen et al., 2014). Similarly, several studies have correlated the presence of *Armatimonadetes* with disease suppression. For instance, significant negative correlations between *Armatimonadetes* with disease index of bacterial wilt were observed in tobacco (Chen et al., 2020) and vanilla (Xiong et al., 2015). Furthermore, the relative abundance of *Armatimonadetes* was found to be enriched following yellow mosaic disease infection in wheat (Wu et al., 2021) and was exclusively associated with the rhizosphere of asymptomatic avocado trees in an orchard infected with Fusarium dieback (Bejarano-Bolívar et al., 2021). Despite these relationships among cover cropping measurements and rotational values, our experimental design was unable to determine if these relationships were correlative or causational. Further experimentation that manipulates the absence and presence of these variables is required to evaluate the true relationship among these variables and rotational value.

4.3 | Breeding a next-generation cover crop

Cover cropping and crop rotations have been used in numerous agroecosystems throughout agricultural history to improve yields and soil quality. The results obtained from this study highlight the significant impacts of genotype on a cover crop performance. Implications from our research suggest that researchers studying cover cropping may now need to narrow to the genotype level rather than the family level (legumes, cereals, etc.). Failing to account for genotypic differences or not incorporating multiple genotypes into studies can result in inaccurate characterization of crops as rotational partners. This can lead to an incomplete understanding of the potential and actual performance of cover crops in crop rotation systems. It would also be useful to look at inoculation with a variety of rhizobia to see if nitrogen fixation increases. Although including multiple rhizobial strains as inoculum was beyond the scope of this study, it is crucial to investigate in future research studies, given that nitrogen fixation represents the primary advantage of legumes in crop rotations. It is crucial for research on cover crops and crop rotations to consider and account for the impact of genotypes on crop performance to ensure that the results accurately reflect the potential of cover crops as sustainable agricultural practices. Furthermore, our research suggests that CWRs should be incorporated into cover crop breeding programs to reintroduce lost beneficial phenotypic and genotypic variation. This can be instrumental in improving cover crop rotational values, which in turn can facilitate the development of more efficient and effective crop rotations that can contribute to meeting the future nutritional needs of a growing human population. Therefore, the integration of CWRs into breeding programs can play a significant role in promoting sustainable agriculture practices that enhance soil quality and crop yields.

AUTHOR CONTRIBUTIONS

Edward Marques: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; visualization; writing—original draft; writing—review and editing. **Lauren Kerwien**: Data curation; investigation; project administration; writing—review and editing. **Erika Bueno**: Data curation; investigation; validation; visualization; writing—review and editing. **Eric Bishop-von Wettberg**: Conceptualization; data curation; funding acquisition; project administration; resources; supervision; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on our Open Science Foundation site for this project (https://osf.io/2kbrf/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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